

Schöb, C., Armas, C. and Pugnaire, F. I. 2013.
Direct and indirect interactions co-determine
species composition in nurse plant systems. –
Oikos 000: 000–000.

Appendix 1

Table A1. Target species for species-level effects in the *Retama sphaerocarpa* and *Arenaria tetraquetra* ssp. *amabilis* nurse plant systems. Mean individual biomass, frequency, abundance, and observed RII as well as nurse and beneficiary effects for each species are shown. RII is based on biomass. Frequency and abundance of each species was obtained in either 16 plots (*R. sphaerocarpa* system), 85 plots (*A. tetraquetra* system, North-Low), or 100 plots (*A. tetraquetra* system, North-High, South-Low, and South-High). Biomass was obtained from ten (in the *R. sphaerocarpa* system) or five (in the *A. tetraquetra* system) individuals per species, size class or site, and microhabitat

Subordinate beneficiary species	Size class / Site	Micro-habitat	Biomass (g)	Frequency	No. of individuals /plot	RII _{observed}	RII _{beneficiary}	RII _{nurse}
<i>Retama sphaerocarpa</i>-system								
<i>Andryala ragusina</i> (Asteraceae)	Small shrub	Open	2.3079	0.063	0.13	-	-	-
		Nurse	2.1875	0.125	0.13	-0.04	-0.52	0.49
	Medium shrub	Open	2.3079	0.063	0.13	-	-	-
		Nurse	2.4953	0.375	1.81	0.04	-0.67	0.69
	Large shrub	Open	2.3079	0.063	0.13	-	-	-
		Nurse	2.7213	0.188	0.31	0.08	-0.69	0.73
<i>Avena sterilis</i> (Poaceae)	Small shrub	Open	0.1327	<0.063	<0.06	-	-	-
		Nurse	0.5787	0.313	0.88	0.49	0.09	0.38

	Medium shrub	Open	0.1327	<0.063	<0.06	-	-	-
		Nurse	1.4873	0.313	3.06	0.76	0.22	0.60
	Large shrub	Open	0.1327	<0.063	<0.06	-	-	-
		Nurse	1.9068	0.625	3.75	0.84	0.34	0.69
<i>Bromus rubens</i>	Small shrub	Open	0.1198	<0.063	<0.06	-	-	-
(Poaceae)		Nurse	0.2079	0.688	3.44	0.18	-0.32	0.42
	Medium shrub	Open	0.1198	<0.063	<0.06	-	-	-
		Nurse	0.2796	0.625	11.88	0.35	-0.43	0.66
	Large shrub	Open	0.1198	<0.063	<0.06	-	-	-
		Nurse	0.5813	0.688	8.56	0.64	-0.16	0.71
<i>Lagurus ovatus</i>	Small shrub	Open	0.1038	<0.063	<0.06	-	-	-
(Poaceae)		Nurse	0.3257	<0.063	<0.06	0.31	-0.10	0.30
	Medium shrub	Open	0.1038	<0.063	<0.06	-	-	-
		Nurse	0.3545	0.063	0.06	0.47	-0.23	0.63
	Large shrub	Open	0.1038	<0.063	<0.06	-	-	-
		Nurse	0.3505	0.438	2.56	0.55	-0.25	0.73
<i>Paronychia argentea</i>	Small shrub	Open	0.1884	0.250	0.56	-	-	-
(Caryophyllaceae)		Nurse	0.3158	0.563	2.69	0.15	-0.27	0.36
	Medium shrub	Open	0.1884	0.250	0.56	-	-	-
		Nurse	0.4631	0.438	2.19	0.31	-0.39	0.59
	Large shrub	Open	0.1884	0.250	0.56	-	-	-
		Nurse	0.3643	0.250	0.50	0.23	-0.46	0.63
<i>Rumex bucephalophorus</i>	Small shrub	Open	0.0779	0.188	0.31	-	-	-
(Polygonaceae)		Nurse	0.1270	0.438	14.31	0.22	-0.29	0.47
	Medium shrub	Open	0.0779	0.188	0.31	-	-	-
		Nurse	0.1088	0.375	1.19	0.13	-0.59	0.65
	Large shrub	Open	0.0779	0.188	0.31	-	-	-
		Nurse	0.1320	0.250	1.44	0.12	-0.60	0.60
<i>Stipa capensis</i>	Small shrub	Open	0.1128	0.938	20.69	-	-	-
(Poaceae)		Nurse	0.2029	1.000	23.38	0.29	-0.23	0.50
	Medium shrub	Open	0.1128	0.938	20.69	-	-	-
		Nurse	0.2104	0.875	11.50	0.26	-0.47	0.66
	Large shrub	Open	0.1128	0.938	20.69	-	-	-
		Nurse	0.4480	0.313	1.00	0.57	-0.22	0.71

Arenaria tetraquetra-system

<i>Eryngium glaciale</i>	North-Low	Open	0.3146	<0.01	<0.01	-	-	-
(Apiaceae)		Nurse	0.0913	0.04	0.04	-0.13	-0.30	0.30
	North-High	Open	0.1070	0.04	0.06	-	-	-
		Nurse	0.0592	0.11	0.21	-0.13	-0.14	0.08
	South-Low	Open	0.3256	<0.01	<0.01	-	-	-
		Nurse	0.0590	0.04	0.05	-0.55	-0.59	0.15
	South-High	Open	0.3027	0.04	0.04	-	-	-
		Nurse	0.1512	0.04	0.05	-0.41	-0.56	0.06
<i>Euphorbia nevadensis</i>	North-Low	Open	0.0188	0.20	0.25	-	-	-
(Euphorbiaceae)		Nurse	0.0242	0.21	0.27	0.08	-0.15	0.21
	South-Low	Open	0.0578	0.27	0.43	-	-	-
		Nurse	0.0542	0.39	0.86	-0.07	-0.13	0.01
<i>Galium pyrenaicum</i>	North-Low	Open	0.3664	0.05	0.05	-	-	-
(Rubiaceae)		Nurse	0.1201	0.14	2.07	-0.39	-0.54	0.12
	North-High	Open	0.3349	0.12	0.57	-	-	-
		Nurse	0.2412	0.27	3.07	-0.20	-0.21	-0.06
	South-Low	Open	0.1519	0.01	0.04	-	-	-
		Nurse	0.0478	0.01	0.02	-0.56	-0.60	-0.08
	South-High	Open	0.1196	0.37	1.84	-	-	-
		Nurse	0.1522	0.54	5.11	0.01	-0.17	0.08
<i>Jasione amethystina</i>	North-Low	Open	0.6618	0.58	1.07	-	-	-
(Campanulaceae)		Nurse	0.3250	0.79	2.67	-0.37	-0.57	0.18
	North-High	Open	0.1835	0.20	0.36	-	-	-
		Nurse	0.3239	0.53	1.90	0.19	0.19	-0.05
	South-Low	Open	0.1777	0.04	0.11	-	-	-
		Nurse	0.3221	0.20	0.48	0.22	0.16	0.04
	South-High	Open	0.3550	0.15	0.32	-	-	-
		Nurse	0.0703	0.58	2.85	-0.67	-0.76	0.12
<i>Leontodon boryi</i>	North-Low	Open	0.1809	0.12	0.21	-	-	-
(Asteraceae)		Nurse	0.2634	0.14	0.15	0.13	-0.15	0.23
	North-High	Open	0.0721	0.01	0.01	-	-	-
		Nurse	0.1047	0.04	0.23	0.16	0.16	-0.01
	South-Low	Open	0.1134	0.11	0.17	-	-	-

		Nurse	0.1619	0.29	0.82	0.16	0.9	0.06
	South-High	Open	0.0791	<0.01	<0.01	-	-	-
		Nurse	0.0727	0.02	0.31	-0.05	-0.24	0.18
<i>Nevadensia purpurea</i>	North-Low	Open	0.2130	0.11	0.14	-	-	-
(Brassicaceae)		Nurse	0.0653	0.08	0.20	-0.51	-0.68	0.18
	North-High	Open	0.3453	0.10	0.13	-	-	-
		Nurse	0.2486	0.13	0.31	-0.05	-0.05	0.12
	South-Low	Open	0.5281	0.05	0.07	-	-	-
		Nurse	0.1994	0.19	0.38	-0.28	-0.33	0.11
	South-High	Open	0.1783	0.68	2.53	-	-	-
		Nurse	0.0772	0.85	4.75	-0.32	-0.48	0.21
<i>Sideritis glacialis</i>	South-High	Open	1.5268	0.05	0.05	-	-	-
(Lamiaceae)		Nurse	0.4035	0.07	0.09	-0.58	-0.69	0.08
<i>Trisetum glaciale</i>	North-High	Open	0.3080	0.05	0.22	-	-	-
(Poaceae)		Nurse	0.3050	0.15	1.48	-0.10	-0.10	-0.10

Appendix 2

Uncoupling direct effects from nurse-mediated indirect effects on the performance of beneficiary species and final community composition in nurse plant systems is a difficult task. Incontrovertible evidence could only be generated by removing either the *effect* of the nurse or the co-occurring beneficiary species without disturbance of the other. However, both effects at a particular point in time are not simply the result of the presence versus absence of each member of the system at that particular moment, but are developed and accumulated through time (Michalet 2006). Therefore, simple removal of either the nurse or co-occurring beneficiary species in nurse plant systems does not remove the whole complex effect of the corresponding member on a particular beneficiary individual. Furthermore, removal of the nurse plant may not be possible without destroying or at least seriously disturbing the beneficiary community. For example in alpine cushion plant communities, beneficiary species grow within the cushion canopy and some species likely even root within the organic material which is trapped within the cushion (Körner 1993). In this case, removal of the cushion would result in complete destruction of the nurse plant system. In light of the difficulties in experimentally studying such direct and indirect interactions in nurse plant systems we suggest here a simplistic non-destructive approach using observational data from a nurse plant system and a neighboring open area without nurse (Fig.A1).

The nurse effect

In order to quantify the nurse effect in the nurse plant system we compared a community of species growing under influence of the nurse with a community in the neighboring open area. As response variable every performance measure that can be determined on individual plants and on the whole community is suitable (e.g. biomass, productivity, reproductive output). The

difference between these communities was then attributed to the effect of the nurse (if other sources of variation such as small-scale environmental heterogeneity can be neglected). Nurse effects can include improvements in resources, but also protection against herbivores and seed predation, or seed trapping to mention a few, all affecting germination, establishment, productivity, survival and overall fitness of beneficiary plants, the number of individuals of a population and the diversity of the community. Here we compared biomass of a community associated to the nurse (= B_n) with that of a community placed in the open (= B_o) in order to quantify the nurse effect (NE) as

$$1) \text{ NE} = \frac{B_n}{B_o}$$

The beneficiary effect

The difference in biomass of a community with nurse from a community without nurse consists in the presence versus absence of the nurse effect (equation 1). In contrast, given that a species occurs both with and without nurse, the difference in biomass between a single beneficiary individual within the community with nurse (= iB_n) from a single individual of the same species growing isolated in the open area (= iB_o) is the result of the nurse effect (NE) and the beneficiary effect of the plants co-occurring with the target individual in the community with nurse (BE). Therefore,

$$2) \frac{iB_n}{iB_o} = \text{NE} \times \text{BE}$$

Here we assume that iB_o is not affected by co-occurring species in the open area, for example due to the very low density of plants in the stressful environments under study. Alternatively, a neighbor removal experiment could be conducted to exclude interferences with other plants. If we further assume that the nurse effect quantified for the whole community is constant

among beneficiary individuals forming the community, then the beneficiary effect (BE) can be calculated as

$$3) \text{ BE} = \frac{\frac{iBn}{iBo}}{NE} = \frac{iBn}{iBo \times NE} = \frac{iBn \times Bo}{iBo \times Bn}$$

The second assumption of a constant nurse effect among all beneficiary species and individuals in a nurse plant system is crucial, and likely a simplification of reality. The outcome of plant-plant interactions is known to be species-specific because of the hypothesized strategic trade-off of species between stress-tolerance and competitive-response ability (Liancourt et al. 2005). On the one hand, stress-tolerant species may profit less from ameliorated growth conditions than stress-intolerant species resulting, indeed, in species-specific direct nurse effects (Liancourt et al. 2005). On the other hand, under ameliorated conditions provided by the nurse competition may be more intense and favor more competitive species (Liancourt et al. 2005). This effect, however, is not related to the direct nurse effect but to the indirect interactions among beneficiaries. Therefore, much of the species-specificity in the outcome of plant-plant interactions in a nurse plant system is likely to be due to indirect interactions among beneficiary species and not due to species-specific differences in the direct nurse effect. In particular in extreme environments, such as in the high alpine and arid ecosystems studied here, most species are not in the optimum of their fundamental niche (Lortie et al. 2004). Under such conditions the ameliorative effect provided by the nurse would most probably be of a benefit for all species – if there would not be any competition for space and resources under the ameliorated conditions. We therefore think that even though the nurse effects may not be the same, they are likely positive and within a rather narrow range of magnitude for all the species in our study systems.

The intensity of direct and indirect plant–plant interactions

In order to assess the intensity of NE and BE with the relative interaction index RII (Armas et al. 2004) we calculated the potential biomass of a target individual either without nurse but with beneficiaries (= iBwn) or with nurse but without beneficiaries (= iBwb) as

$$4) \text{ iBwn} = \frac{\text{iBn}}{\text{NE}}$$

$$5) \text{ iBwb} = \frac{\text{iBn}}{\text{BE}}$$

The intensities of the direct nurse effect ($\text{RII}_{\text{nurse}}$) and the indirect beneficiary effect ($\text{RII}_{\text{beneficiaries}}$) were then calculated as

$$6) \text{ RII}_{\text{nurse}} = \frac{\text{iBwb} - \text{iBo}}{\text{iBwb} + \text{iBo}}$$

$$7) \text{ RII}_{\text{beneficiaries}} = \frac{\text{iBwn} - \text{iBo}}{\text{iBwn} + \text{iBo}}$$

References

- Armas, C. et al. 2004. Measuring plant interactions: new comparative index. – *Ecology* 85: 2682–2686.
- Körner, C. 1993. Das “Ökosystem Polsterpflanze“: Recycling und Airconditioning. – *Biologie in unserer Zeit* 23: 353–355.
- Liancourt, P. et al. 2005. Stress tolerance and competitive-response ability determine outcome of biotic interactions. – *Ecology* 86: 1611–1618.
- Lortie, C. J. et al. 2004. The value of stress and limitation in an imperfect world: a reply to Körner. – *J. Veg. Sci.* 15: 577–580.
- Michalet, R. 2006. Is facilitation in arid environments the result of direct or complex interactions? – *New Phytol.* 169: 3–6.

Figure A1. Framework for uncoupling indirect beneficiary effects from direct nurse effects in observational data. See text for further explanations and abbreviations.

