

Ecography

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Climate change shifts environmental space and limits
transferability of treeline models. – *Ecography* 36:
xxx–xxx.

Supplementary material

Appendix 1. Study area characteristics and stand basal area distribution.

Table A1 Study area characteristics for the NFI 7, NFI 9_N and NFI 9_S datasets.

	NFI 7	NFI 9 _N	NFI 9 _S
inventory year	1978	2003	2002/ 2003
sample size	217	773	3206
latitude	68.2°– 70.0°N	68.2°– 70.0°N	65.7°– 68 .2°N
longitude	23.1°– 29.2°E	22.4°– 29.2°E	22.4°– 29.3°E
altitude [m a.s.l.]	70.0 – 560.0	73.9 – 565.8	0.0 – 490.1
stand basal area [m ² ha ⁻¹]	0.5 – 20.0	0.0 – 32.0	0.0 – 37.0

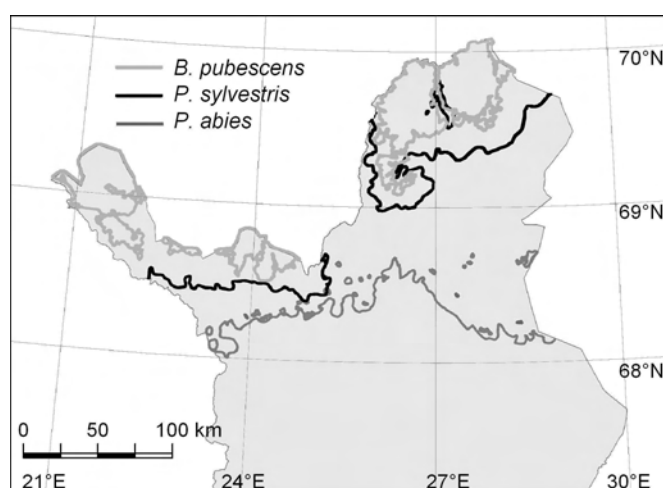


Fig. A1.1 Current treeline positions of *Pinus sylvestris*, *Picea abies* and *Betula pubescens* in Finnish Lapland (based on nature survey data by Metsähallitus, 1996–1999).

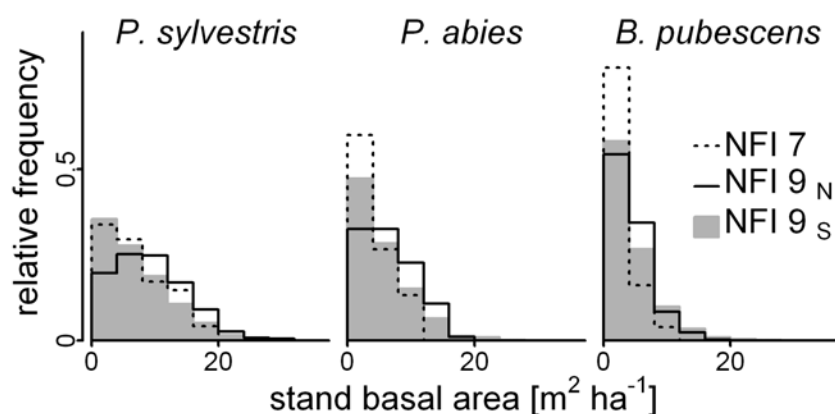


Fig. A1.2 Distribution of stand basal area [m² ha⁻¹] above zero according to species and dataset.

Appendix 2. Methodological details on boosted regression trees.

Table A2 Characteristics of the single boosted regression tree (BRT) models for occurrence and abundance.

	occurrence model			abundance model		
distribution (family)	Bernoulli			Laplace		
response variable	0 / 1			truncated ¹ basal areas		
fitted values	p (y > 0)			basal area [m ² ha ⁻¹]		
range	[0 , 1]			[MIN , MAX]		
number of observations	NFI 7	NFI 9 _N	NFI 9 _S	NFI 7	NFI 9 _N	NFI 9 _S
<i>P. sylvestris</i>	217	773	3206	162	567	2391
<i>P. abies</i>	217	773	3206	15 ²	92	1709
<i>B. pubescens</i>	217	773	3206	148	377	1458
learning rate ³	0.001	0.005	0.005	0.001	0.001	0.005
tree complexity ⁴	5			5		
bag fraction	0.5			0.5		
number of trees ⁵	NFI 7	NFI 9 _N	NFI 9 _S	NFI 7	NFI 9 _N	NFI 9 _S
<i>P. sylvestris</i>	2600	1550	2850	5150	4200	2950
<i>P. abies</i>	2950	1950	8250	– ²	3700	2550
<i>B. pubescens</i>	2000	1150	3350	2200	6550	3250

¹ response vector shortened by the amount of original zeros (i.e. sites without this species)

² sample size too small for model building

³ the learning rate (shrinkage) determines the contribution of each tree to the final ensemble model and, thus, the speed of gradient descent

⁴ the tree complexity (i.e. maximum number of splits in a tree) relates to the interaction depth that can be potentially modelled

⁵ the number of trees is influenced by the two measures above and was determined by cross-validation (Elith et al. 2008)

Literature Cited

Elith, J. et al. 2008. A working guide to boosted regression trees. — J. Anim. Ecol. 77: 802-813.

Appendix 3. Methodological details on the transferability index.

Transferability index (TI) as developed by Randin et al. (2006) and extended by Dobrowski et al. (2011), where GOF can be any goodness-of-fit measure (originally: AUC) and Δ_{MAX} is the maximum difference between internal (IE) and external (EE) evaluation (originally: 0.5 for AUC). The index ranges from 0 (maximum difference between IE and EE, no transferability) to 1 (no difference, full transferability).

$$TI = \frac{0.5 \left(\left(1 - \frac{|GOF_{A \rightarrow A} - GOF_{A \rightarrow B}|}{\Delta_{MAX}} \right) + \left(1 - \frac{|GOF_{B \rightarrow B} - GOF_{B \rightarrow A}|}{\Delta_{MAX}} \right) \right)}{1 + \left| \frac{GOF_{A \rightarrow A} - GOF_{A \rightarrow B}}{\Delta_{MAX}} \right| + \left| \frac{GOF_{B \rightarrow B} - GOF_{B \rightarrow A}}{\Delta_{MAX}} \right|}$$

with A = region A or time 1
B = region B or time 2

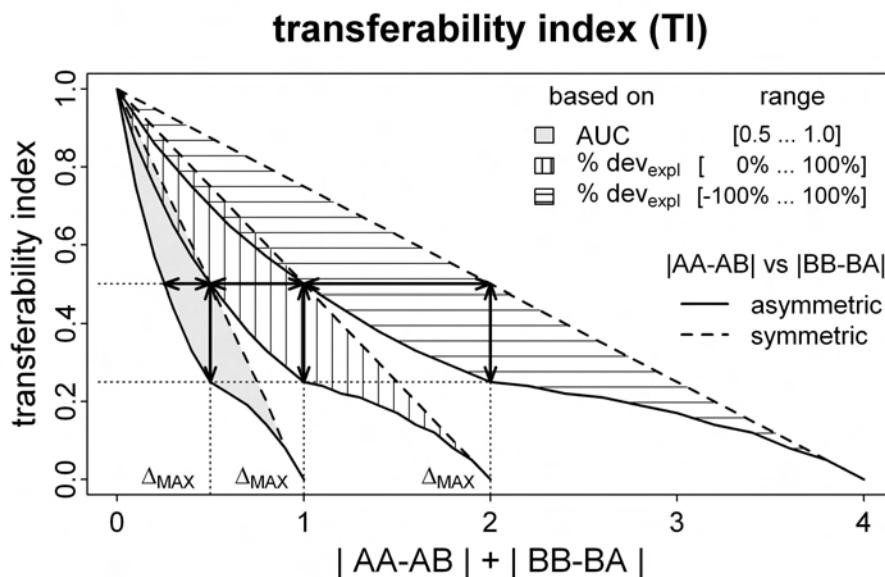


Fig. A3 Transferability index (TI) values based on AUC or percentage of deviance explained (% dev_{expl}) as a function of the sum of absolute differences (|AA-AB|+|BB-BA|) between internal (AA, BB) and external evaluation (AB, BA). The range of possible values (top right corner) corresponds to Δ_{MAX} in the equation above (e.g. 0.5 for AUC). TI = 0 where |AA-AB|+|BB-BA| = 2 Δ_{MAX} (e.g. 1.0 for AUC). For equal sums of absolute differences, TI is higher if the two differences (= directions of model transfer) are similar (symmetric, broken line) as opposed to very different (asymmetric, solid line). Although the range of possible TI values (depending on the symmetry) for a given sum of absolute differences stays the same in all three applications (vertical arrows for Δ_{MAX}), the range of sum of absolute differences leading to the same TI value (horizontal arrows for TI = 0.5) increases (lowest for AUC, highest for a range of -100–100 % dev_{expl}). That makes TI values based on % dev_{expl} harder to interpret and compare with one another than TI values based on AUC.

Literature Cited

- Dobrowski, S. Z. et al. 2011. Modeling plant ranges over 75 years of climate change in California, USA: temporal transferability and species traits. — *Ecol. Monogr.* 81: 241-257.
- Randin, C. F. et al. 2006. Are niche-based species distribution models transferable in space? — *J. Biogeogr.* 33: 1689-1703.

Appendix 4. Visualization of model performance, maps of model predictions, and validation results.

Table A4.1 Intercept (ideally: 0) and slope (ideally: 1) of the calibration curve (Swets 1988) for the internal (IE) and external (EE) evaluation of the occurrence model.

			<i>P. sylvestris</i>		<i>P. abies</i>		<i>B. pubescens</i>	
	trained on	applied to	mean	sd ¹	mean	sd	mean	sd
intercept								
IE (10-fold CV)	NFI 7	NFI 7	-5.563	(5.319)	30.018	(19.087)	-0.394	(0.362)
	NFI 9 _N	NFI 9 _N	0.078	(0.171)	0.906	(0.527)	0.027	(0.040)
	NFI 9 _S	NFI 9 _S	-0.047	(0.053)	0.009	(0.035)	0.016	(0.032)
EE (temporal)	NFI 7	NFI 9 _N	-1.446		2.392		-1.818	
	NFI 9 _N	NFI 7	0.380		-0.818		0.528	
EE (spatial)	NFI 9 _N	NFI 9 _S	0.394		0.943		0.241	
	NFI 9 _S	NFI 9 _N	-0.342		-2.345		0.373	
slope								
IE (10-fold CV)	NFI 7	NFI 7	7.599	(6.380)	19.408	(11.520)	1.333	(0.352)
	NFI 9 _N	NFI 9 _N	1.523	(0.320)	1.358	(0.190)	1.098	(0.052)
	NFI 9 _S	NFI 9 _S	1.028	(0.036)	0.964	(0.036)	1.031	(0.049)
EE (temporal)	NFI 7	NFI 9 _N	1.289		1.180		1.661	
	NFI 9 _N	NFI 7	0.385		0.636		0.377	
EE (spatial)	NFI 9 _N	NFI 9 _S	0.635		0.326		0.754	
	NFI 9 _S	NFI 9 _N	1.549		0.807		1.294	

¹ mean and standard deviation of 10-fold cross-validation

Table A4.2 Pearson and Spearman correlation between observations and predictions

		<i>P. sylvestris</i>		<i>P. abies</i>		<i>B. pubescens</i>	
trained on	applied to	Pearson	Spearman	Pearson	Spearman	Pearson	Spearman
internal evaluation (10-fold CV)							
NFI 7	NFI 7	0.88	0.89	– ¹	–	0.63	0.64
NFI 9 _N	NFI 9 _N	0.92	0.94	0.93	0.56	0.82	0.81
NFI 9 _S	NFI 9 _S	0.79	0.83	0.82	0.82	0.76	0.72
external evaluation: temporal transfer							
NFI 7	NFI 9 _N	0.65	0.70	–	–	0.49	0.54
NFI 9 _N	NFI 7	0.75	0.74	0.35	0.28	0.41	0.41
external evaluation: spatial transfer							
NFI 9 _N	NFI 9 _S	0.68	0.70	0.50	0.42	0.48	0.47
NFI 9 _S	NFI 9 _N	0.79	0.83	0.64	0.40	0.66	0.66

¹ prevalence of *P. abies* in the NFI 7 dataset too small for model building

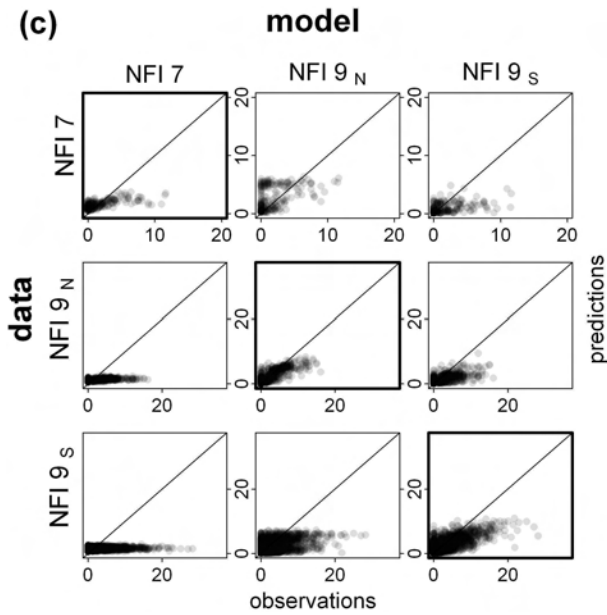
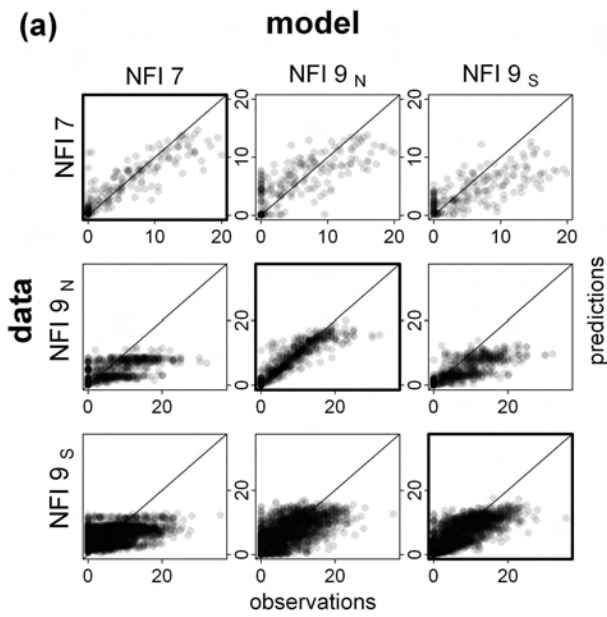


Fig. A4.1 Scatterplots of observations and predictions for each model–data combination for *P. sylvestris* (a), *P. abies* (b) and *B. pubescens* (c); e.g. top right figure in each panel shows NFI 9_S model predictions for NFI 7 data. Main diagonal: internal evaluation cases. *Note:* Prevalence of *P. abies* in the NFI 7 dataset was too small for model building (left column in (b)).

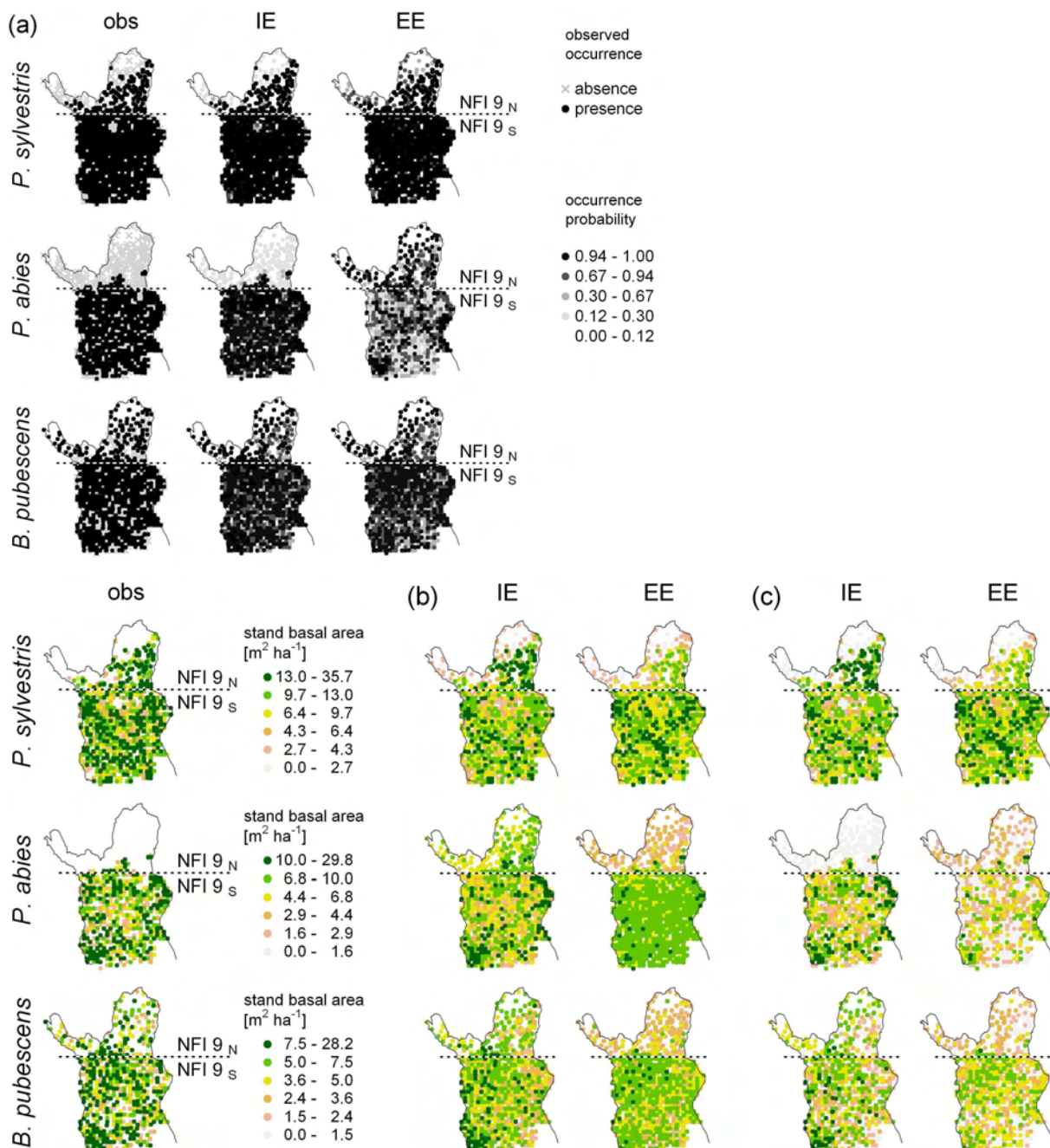


Fig. A4.2 Maps of occurrence (a), abundance (b) and final model (c) predictions for the spatial model transfer: observations (obs); results of the internal evaluation (IE), i.e. northern predictions by NFI 9_N, southern predictions by NFI 9_S model; results of the external evaluation (EE), i.e. northern predictions by NFI 9_S model and southern predictions by NFI 9_N model. Note: basal area is already underestimated by the abundance model; it is not an effect of multiplying the two model results to obtain the final model predictions.

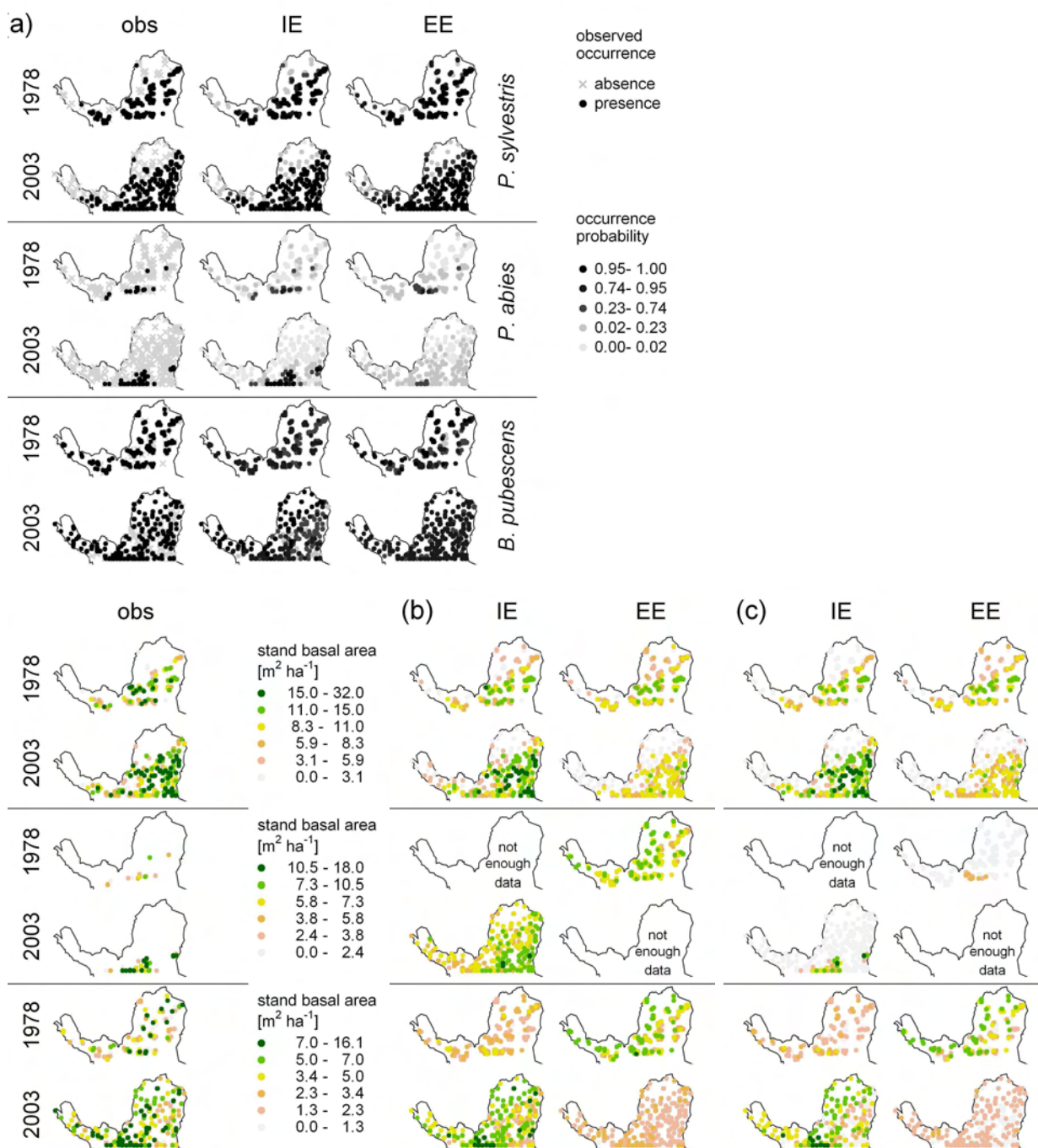


Fig. A4.3 Maps of occurrence (a), abundance (b) and final model (c) predictions for the temporal model transfer: observations (obs); results of the internal evaluation (IE), i.e. 1978 predictions by NFI 7, 2003 predictions by NFI 9_N model; results of the external evaluation (EE), i.e. 1978 predicted by NFI 9_N model (hindcasting) and 2003 predicted by NFI 7 model (forecasting).

Literature Cited

Swets, J. A. 1988. Measuring the accuracy of diagnostic systems. — Science 240: 1285-1293.

Appendix 5. Analysis of the automatically fitted interactions between predictors.

Table A5.1 Ten most important interactions for each model. The four most important predictors (identified on the basis of relative importance) are marked in bold ¹.

NFI7		NFI9 _N		NFI9 _S	
occurrence	abundance	occurrence	abundance	occurrence	abundance
<i>P. sylvestris</i>					
GDD – TPI	B.pub – fert	P.abi – B.pub	P.abi – fert	P.abi – B.pub	P.abi – B.pub
fert – GDD	fert – P_Aug	B.pub – GDD	B.pub – fert	P.abi – GDD	P.abi – fert
B.pub – P_May	fert – GDD	P.abi – GDD	fert – GDD	GDD – P_Aug	B.pub – fert
GDD – TRASP	fert – P_May	B.pub – fert	fert – P_May	B.pub – fert	fert – SBI
B.pub – TWI	B.pub – P_May	B.pub – AFI	P.abi – B.pub	B.pub – GDD	fert – TRASP
GDD – TWI	fert – TPI	P.abi – fert	fert – AFI	P.abi – P_May	P.abi – TRASP
fert – TWI	fert – SBI	GDD – TPI	GDD – TWI	GDD – SBI	fert – AFI
GDD – P_May	fert – AFI	B.pub – TPI	B.pub – AFI	P.abi – fert	P_Aug – TWI
B.pub – GDD	B.pub – GDD	P.abi – P_May	GDD – SBI	P_May – SBI	B.pub – TWI
SBI – AFI	fert – TRASP	P.abi – AFI	AFI – TPI	P_Aug – SBI	TRASP – TWI
<i>P. abies</i>					
AFI – TWI	–	P.syl – P_May	B.pub – fert	P.syl – SBI	P.syl – B.pub
P.syl – fert	–	AFI – SBI	P.syl – B.pub	B.pub – TPI	P.syl – fert
P.syl – GDD	–	fert – P_May	P.syl – fert	B.pub – AFI	P.syl – GDD
AFI – TPI	–	fert – AFI	B.pub – TRASP	P.syl – GDD	GDD – AFI
AFI – P_May	–	P.syl – B.pub	fert – SBI	SBI – TWI	B.pub – fert
P.syl – AFI	–	B.pub – AFI	B.pub – AFI	P_May – TRASP	B.pub – GDD
SBI – TRASP	–	P.syl – fert	B.pub – TWI	fert – TPI	fert – P_Aug
AFI – SBI	–	TPI – TRASP	fert – AFI	P.syl – B.pub	fert – GDD
P.syl – SBI	–	AFI – P_May	fert – TWI	GDD – TPI	GDD – SBI
fert – TRASP	–	AFI – TPI	B.pub – TPI	B.pub – TWI	B.pub – SBI
<i>B. pubescens</i>					
fert – AFI	TPI – TWI	P.syl – P.abi	P.syl – P.abi	P.abi – GDD	P.syl – P.abi
P.syl – fert	GDD – TWI	P.syl – fert	P.syl – fert	P.syl – P.abi	P.syl – fert
P.syl – P_May	P.syl – P_Aug	P.syl – AFI	P.syl – AFI	SBI – TWI	P.syl – P_May
fert – GDD	P.syl – TWI	P.syl – GDD	P.syl – TRASP	P.abi – TWI	P_Aug – TWI
P_May – TRASP	AFI – TWI	P.syl – P_Aug	P.syl – P_Aug	P.syl – fert	P.abi – fert
P.syl – TRASP	P.syl – P_May	fert – P_Aug	P.syl – SBI	SBI – AFI	fert – AFI
TWI – TRASP	P_May – TRASP	P.abi – fert	P.syl – P_May	fert – TWI	fert – TWI
TWI – P_May	P.syl – AFI	GDD – AFI	P_Aug – TRASP	P_May – SBI	P.syl – TWI
TWI – SBI	TPI – TRASP	P.syl – TRASP	P.syl – TPI	P.abi – AFI	fert – TPI
fert – TWI	P.syl – SBI	fert – SBI	AFI – TWI	SBI – TPI	P.syl – SBI

¹ GDD – growing degree days; fert – site fertility; P.syl – *P. sylvestris* basal area [m²ha⁻¹]; P.abi – *P. abies* basal area [m²ha⁻¹]; B.pub – *B. pubescens* basal area [m²ha⁻¹]

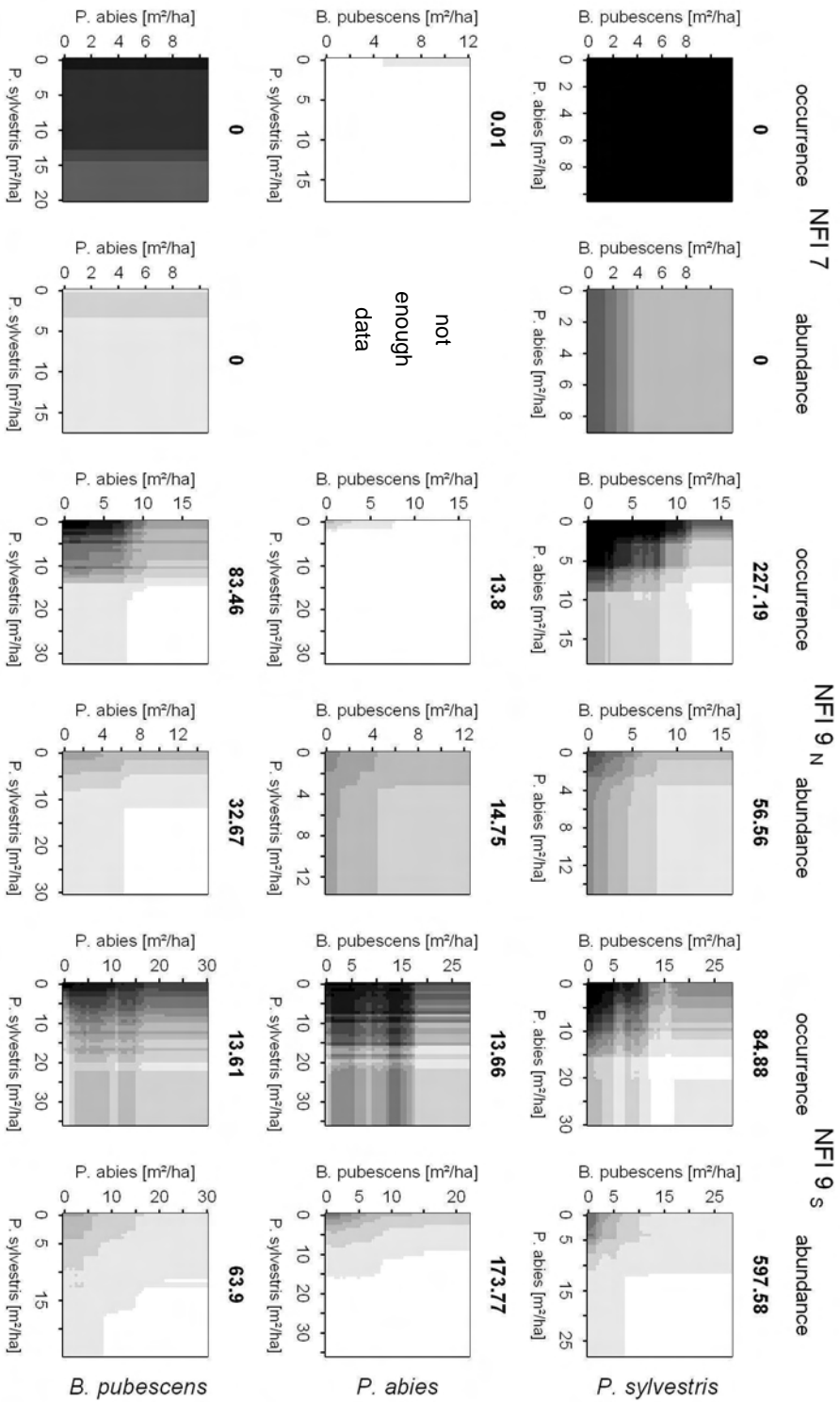


Fig. A5.1 The interaction between the two co-occurring species in all models for *P. sylvestris* (top row), *P. abies* (middle row) and *B. pubescens* (bottom row). Figures above each plot are the respective interaction magnitude from Tables A5.2 to A5.4. Grey shades range from white (occurrence probability of 0; abundance of 0 m² ha⁻¹) to black (occurrence probability of 1; abundance of 20 m² ha⁻¹).

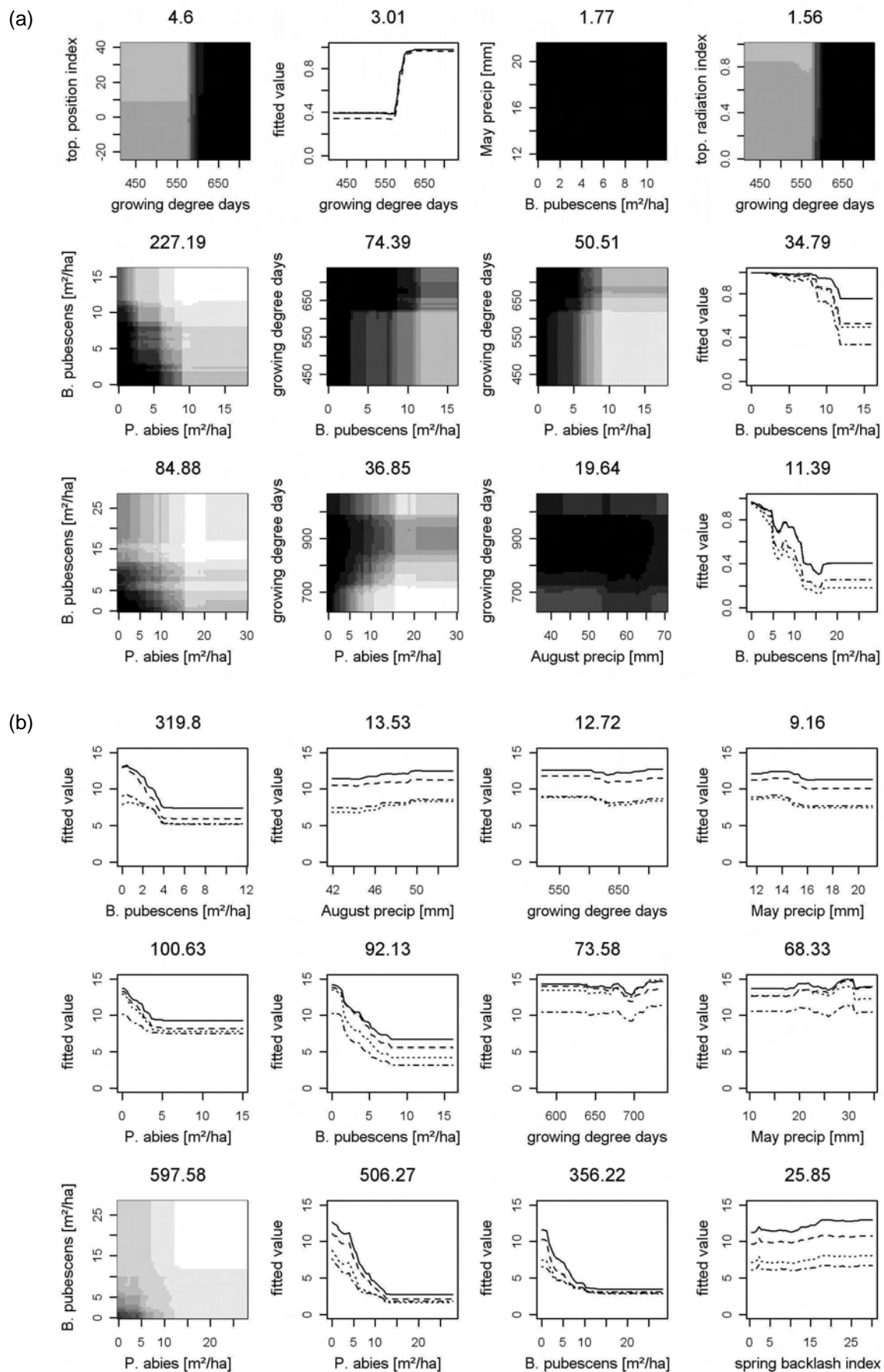
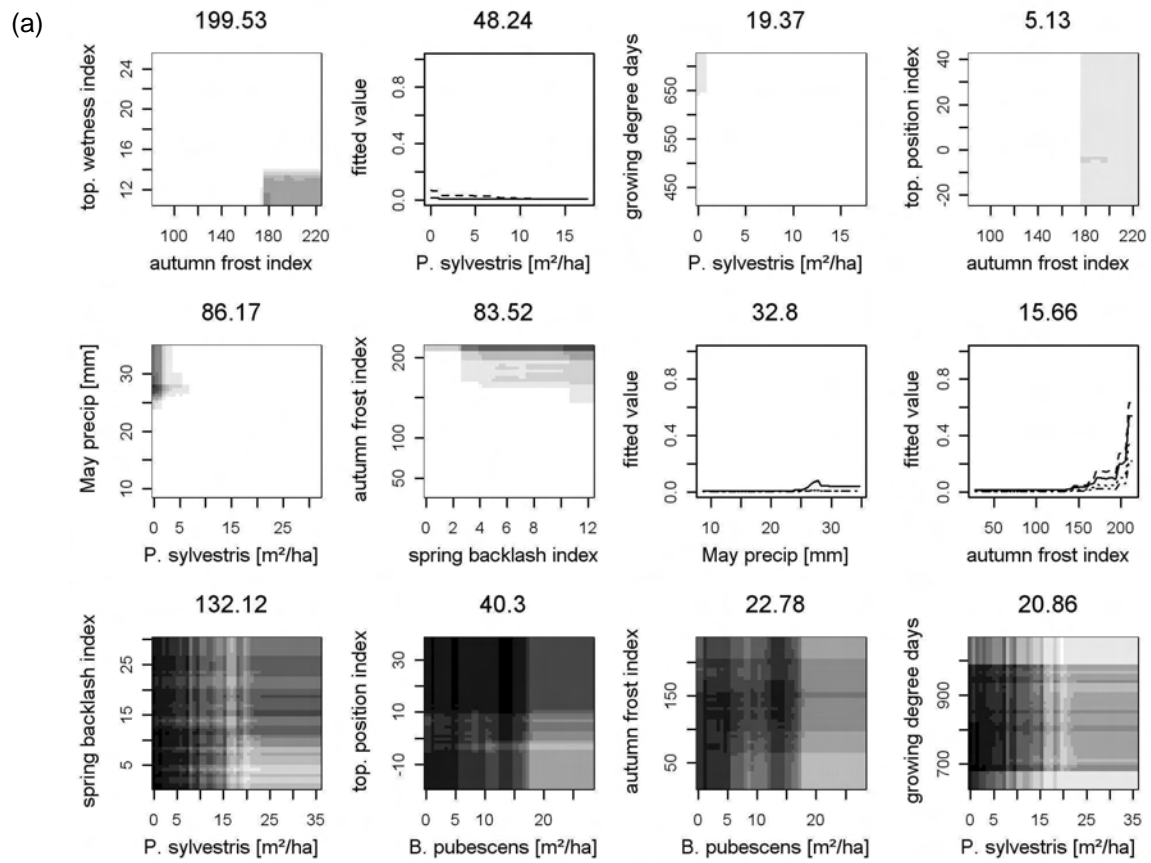


Fig. A5.2 The four most important interactions in the *P. sylvestris* occurrence (a) and abundance (b) models (top row: NFI 7, middle row: NFI 9_N, bottom row: NFI 9_S). Figures above each plot are the respective interaction magnitude from Table A5.2. Site fertility classes are 1 – solid, 2 – dashed, 3 – dotted, 4 – dotdash. Grey shades for continuous combinations range from white (occurrence probability of 0; abundance of 0 m² ha⁻¹) to black (occurrence probability of 1; abundance of 15 m² ha⁻¹).



(b) **NFI 7** (sample size too small for model building)

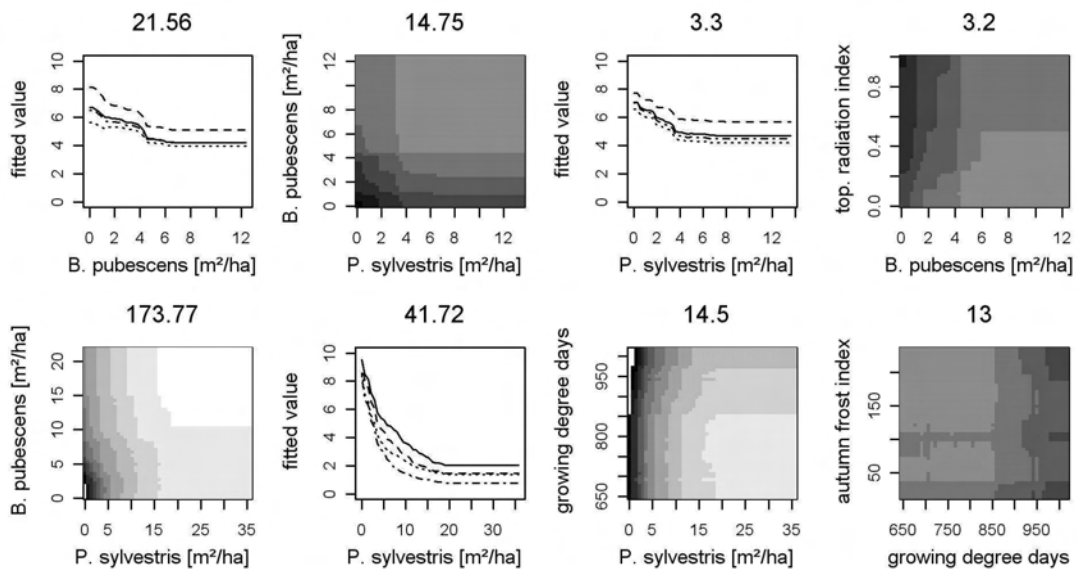


Fig. A5.3 The four most important interactions in the *P. abies* occurrence (a) and abundance (b) models (top row: NFI 7, middle row: NFI 9_N, bottom row: NFI 9_S). Figures above each plot are the respective interaction magnitude from Table A5.3. Site fertility classes are 1 – solid, 2 – dashed, 3 – dotted, 4 – dotdash. Grey shades for continuous combinations range from white (occurrence probability of 0; abundance of 0 m² ha⁻¹) to black (occurrence probability of 1; abundance of 10 m² ha⁻¹).

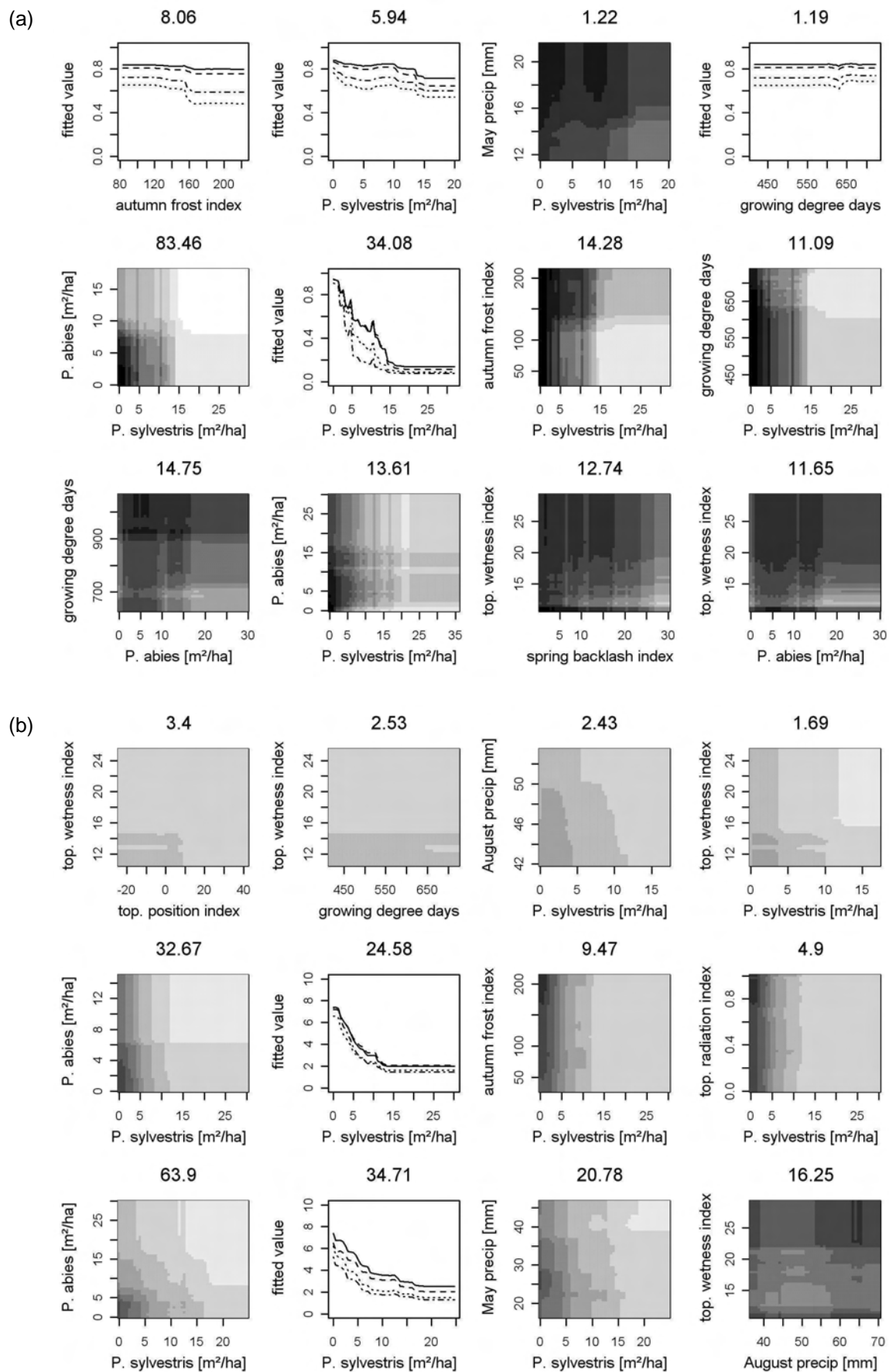


Fig. A5.4 The four most important interactions in the *B. pubescens* occurrence (a) and abundance (b) models (top row: NFI 7, middle row: NFI 9_N, bottom row: NFI 9_S). Figures above each plot are the respective interaction magnitude from Table A5.4. Site fertility classes are 1 – solid, 2 – dashed, 3 – dotted, 4 – dotdash. Grey shades for continuous combinations range from white (occurrence probability of 0; abundance of 0 m² ha⁻¹) to black (occurrence probability of 1; abundance of 10 m² ha⁻¹).

Literature Cited

Hijmans, R. J. et al. 2012. dismo: Species distribution modeling. — R package version 0.7-17 <http://CRAN.R-project.org/package=dismo>.

Appendix 6. Detailed insights into specific predictors, their relationships and relative importance.

Table A6 Spearman correlation of autumn frost index (AFI) and each predictor (corr), changes in relative importance [%] when AFI is omitted (without – with AFI, Δ_{contr}) as well as interaction size ¹ (inter) of AFI and each predictor for the *P. abies* occurrence model.

	NFI 7			NFI 9 _N			NFI 9 _S		
	corr	Δ_{contr}	inter	corr	Δ_{contr}	inter	corr	Δ_{contr}	inter
growing degree days	0.16	2	0.02	0.16	6	5.18	0.03	0	0.89
<u>spring backlash index</u>	0.40	7	1.52	-0.48	-3	<u>83.52</u>	-0.03	0	11.04
May precipitation	0.09	1	4.16	-0.30	9	10.25	-0.58	0	1.41
August precipitation	-0.49	9	0.03	0.02	0	1.26	-0.30	0	4.06
topogr. radiation index	-0.05	4	0.36	0.01	2	2.64	0.03	0	3.11
topogr. position index	-0.04	4	5.13	0.09	-1	10.06	0.01	0	9.95
<u>topogr. wetness index</u>	0.23	-4	<u>199.53</u>	0.30	-1	1.12	0.23	1	4.23
<i>P. sylvestris</i> ²	0.24	9	3.73	-0.10	6	5.79	-0.05	-1	2.03
<i>B. pubescens</i> ²	-0.04	1	0.01	0.09	-2	12.91	0.08	0	22.78
site fertility	–	4	0.71	–	1	15.66	–	0	1.09

¹ interaction size assessed with function `gbm.interactions` from *dismo* package version 0.7-17 (Hijmans et al. 2012)

² basal area [m² ha⁻¹] of co-occurring species

Bold marks higher correlation and thus higher changes in relative importance when AFI is omitted; underlined marks strong interactions leading to a loss of relative importance (negative Δ_{contr}) when AFI is omitted.

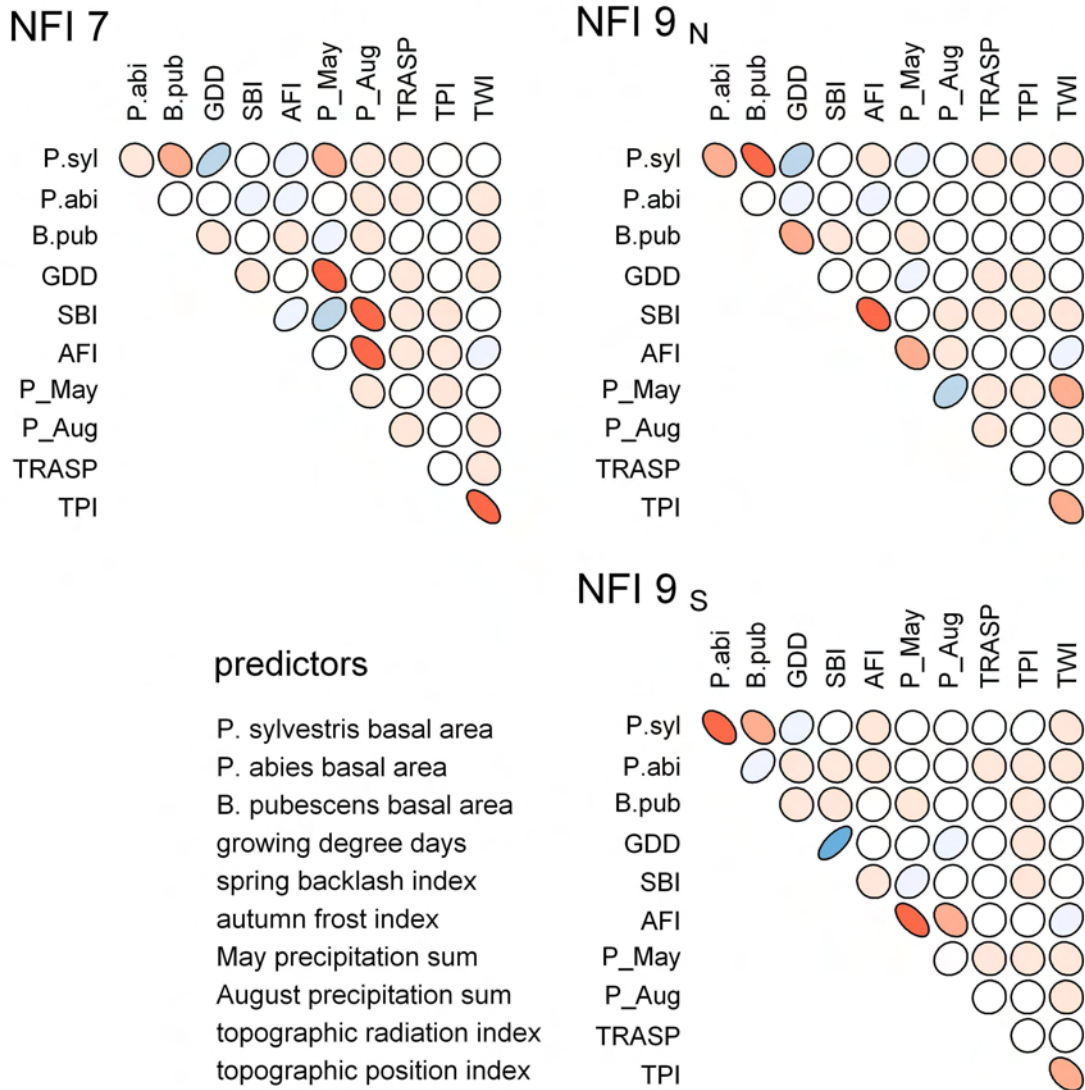


Fig. A6.1 Spearman correlation between predictors of the NFI 7, NFI 9_N and NFI 9_S datasets. Form of the ellipse and shade of colour (red: negative, blue: positive) increase with increasing correlation index values. White circle denotes no correlation (Spearman index = 0). TWI = topographic wetness index.

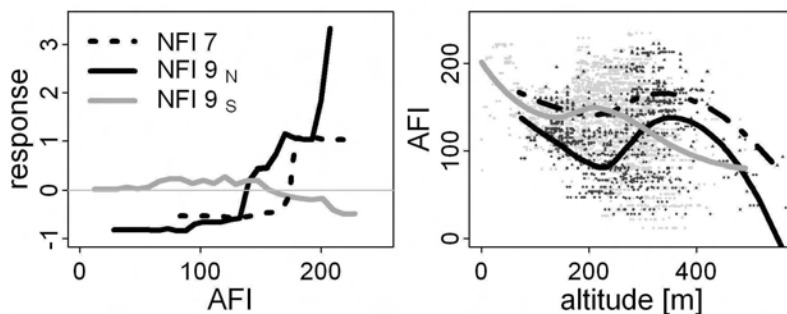


Fig. A6.2 Response curves for the autumn frost index (AFI) in the *P. abies* occurrence model (left) and scatterplot of AFI and altitude with loess curves for the NFI 7, NFI 9_N and NFI 9_S datasets (right).

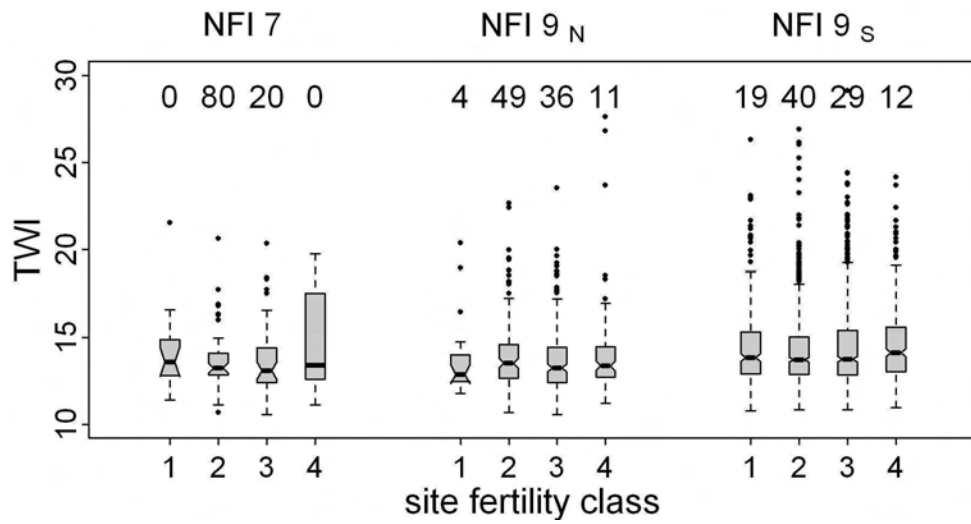


Fig. A6.3 Distribution of the topographic wetness index (TWI) in each site fertility class in the NFI 7, NFI 9_N and NFI 9_S dataset. Numbers above the boxplots give the percentage of *P. abies* presences in that class.

Literature Cited

Hijmans, R. J. et al. 2012. dismo: Species distribution modeling. — R package version 0.7-17 <http://CRAN.R-project.org/package=dismo>.

Appendix 7. Comparison of abundance models trained with and without absences.

Model performance generally improves for internal model validation when absences are included in the model training (Table A7.1). However, model performance on external datasets deteriorates, especially for *P. abies* and *B. pubescens*. Thus, model transferability is lower for these species.

We chose to train abundance models on presence-only data because that better distinguishes abundance from occurrence effects. The relative importance of predictors (Table A7.2) as well as response curves (Fig.A7.1) change when absences are included, which we ascribe to the underlying occurrence effect now mixed with the abundance effect.

Table A7.1 Explained deviances for the abundance models trained on presence-only data (as in the manuscript) vs. data including absences, and transferability index based on explained deviance for temporal and spatial transferability.

		<i>P. sylvestris</i>			<i>P. abies</i>			<i>B. pubescens</i>		
train	test	abund	final	abund	abund	final	abund	abund	final	abund
		presence-only			presence-only			presence-only		
internal evaluation (10-fold CV)										
NFI 7	NFI 7	36.0	33.7	45.8	–	–	–	10.0	6.5	11.1
NFI 9 _N	NFI 9 _N	38.1	44.1	56.2	12.7	43.6	52.4	16.8	25.3	43.4
NFI 9 _S	NFI 9 _S	33.2	32.8	41.8	27.5	22.9	40.9	22.0	24.0	36.2
external evaluation: temporal transfer										
NFI 7	NFI 9 _N	-2.8	3.6	3.6	–	–	–	-24.7	-16.8	-48.8
NFI 9 _N	NFI 7	34.7	24.0	39.0	-34.1	2.1	-60.4	-14.0	-11.6	-5.9
external evaluation: spatial transfer										
NFI 9 _N	NFI 9 _S	18.7	20.7	19.9	-7.0	-38.9	-22.7	9.5	10.1	-8.1
NFI 9 _S	NFI 9 _N	4.9	18.4	2.3	19.8	-41.4	7.3	6.3	20.4	-18.4
transferability index based on % dev _{expl}										
NFI 7 ↔ NFI 9 _N		0.67	0.77	0.71	–	–	–	0.73	0.72	0.62
NFI 9 _N ↔ NFI 9 _S		0.77	0.82	0.75	0.82	0.43	0.53	0.86	0.86	0.66

Grey figures mark cases where the model is weaker than the null model (negative dev_{expl}).

Table A7.2 Difference between the relative importance [%] of the predictors in the abundance model trained on presence-only data and trained with absences.

	<i>P. sylvestris</i>			<i>P. abies</i>			<i>B. pubescens</i>		
	NFI7	NFI9 _N	NFI9 _S	NFI7	NFI9 _N	NFI9 _S	NFI7	NFI9 _N	NFI9 _S
GDD	+ 5	+ 1	0	–	0	– 2	– 3	– 2	– 4
SBI	– 2	– 2	– 1	–	– 5	– 1	+ 4	– 2	– 4
AFI	– 1	– 4	– 1	–	+ 3	– 1	– 5	+ 1	– 1
May prec	– 3	– 3	0	–	+ 8	– 2	+ 4	– 2	– 4
Aug prec	0	– 2	– 1	–	+ 1	– 1	– 5	– 5	– 3
TRASP	– 1	– 4	– 2	–	– 7	– 2	+ 4	– 3	– 3
TPI	– 1	– 2	– 1	–	– 1	0	– 5	– 1	– 1
TWI	0	– 2	– 2	–	– 5	– 2	– 10	– 2	– 5
species ₁ ¹	0	+ 7	+ 12	–	+ 27	+ 13	– 2	+ 13	+ 21
species ₂ ²	– 6	+ 12	+ 8	–	– 16	– 1	0	+ 4	+ 2
fertility	+ 9	– 1	– 12	–	– 5	– 3	+ 18	– 1	+ 2

Bold figures mark the greatest changes.

¹ i.e. *P. abies* in *P. sylvestris*' case and *P. sylvestris* for *P. abies* and *B. pubescens* models

² i.e. *P. abies* in *B. pubescens*' case and *B. pubescens* for *P. sylvestris* and *P. abies* models

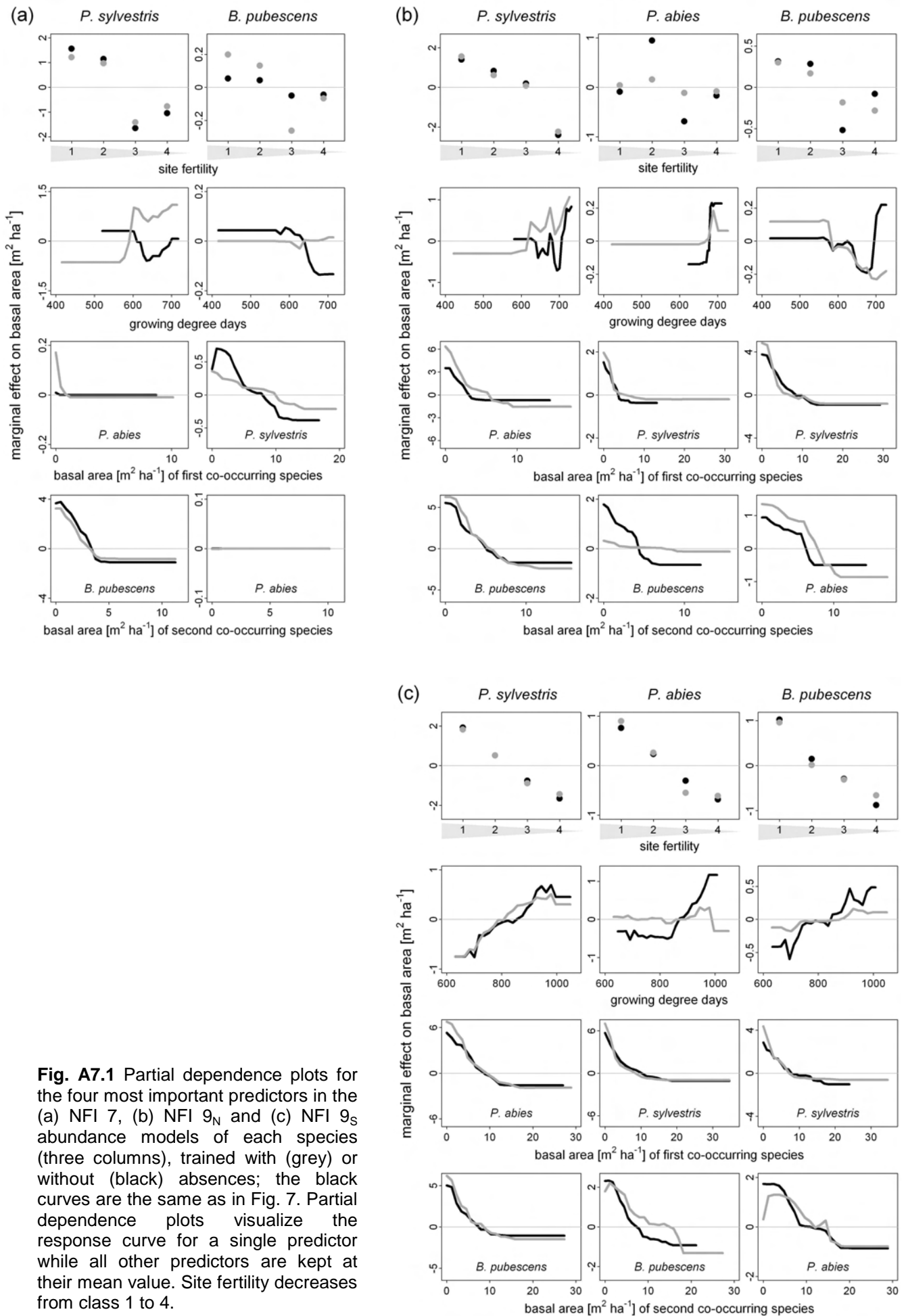


Fig. A7.1 Partial dependence plots for the four most important predictors in the (a) NFI 7, (b) NFI 9_N and (c) NFI 9_S abundance models of each species (three columns), trained with (grey) or without (black) absences; the black curves are the same as in Fig. 7. Partial dependence plots visualize the response curve for a single predictor while all other predictors are kept at their mean value. Site fertility decreases from class 1 to 4.