

# Population genetics of a frog you've never heard of

By

EVAN E. BATZER

DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

ECOLOGY

in the

OFFICE OF GRADUATE STUDIES

of the

UNIVERSITY OF CALIFORNIA  
DAVIS

Approved:

---

(Valerie Eviner), Chair

---

(Susan Harrison)

---

(Andrew Latimer)

Committee in Charge

2020

“My dedication”

## Acknowledgements

“My acknowledgments”

Evan E. Batzer  
October 2020  
ECOLOGY

## **Abstract**

“Frogs are great. Ribbit Ribbit.”

# Contents

Abstract	iv
List of Tables	vii
List of Figures	viii
1 UCD thesis fields	1
2 The “Neutral Theory” of Niche Dimensionality	2
3 Nitrogen enrichment has scale-dependent effects on plant diversity in California grasslands.	3
4 Climate drives transitions between vegetation states in California grasslands.	4
Abstract . . . . .	5
Introduction . . . . .	5
Methods . . . . .	5
Results . . . . .	5
Discussion . . . . .	5
Conclusion	6
A Supporting information for Chapter 1	7
B Supporting information for Chapter 2	11

C Supporting information for Chapter 3	12
References	18

# List of Tables

A.1	Table of sites included in analysis. . . . .	9
A.2	Table of sites, pairwise correlations between community responses to different treatments ( $\rho$ ), rate of community change in response to treatment ( $\Delta$ ), and estimated response dimensionality (D). Significant ( $P < 0.05$ ) magnitudes of community response are labelled with *. . . . .	10
C.1	Heuristics used to determine best number of clusters to use in partitioning, K. Summary of the best performing K for 8 different clustering indices. .	12
C.2	Rank summary table of performance across different clustering indices. .	12
C.3	Contingency table of observed transitions between state assignments between 2008-2018. For each plot observation of a state assignment in year $t$ (rows), data shows the frequency of state assignments (columns) of the same plot in a subsequent year ( $t + 1$ ). Diagonal values represent the frequency of a given state retaining its assignment (persistence), while off-diagonal values represent transitions in state assignment. Changes in assignment frequency were highly non-random ( $\chi^2 = 392.017$ , $df = 9$ , $P < 0.001$ ). . . . .	14
C.4	AIC model comparison used to select the best fit multi-state model from a series of candidates. Covariates include “Priority Effects” – the effect of initial seeding mixture representation of indicator species correlated with cluster assignments – and “1-“, “2-“, and “3-year SPEI” – a standardized measure of drought stress computed over 1, 2, and 3 cumulative water year intervals, respectively. DF corresponds to the number of parameters estimated within the transition matrix, including baseline transition probabilities and effects of covariates. . . . .	14

# List of Figures

A.1	Bivariate relationships between treatments colored by species lifespan. . . . .	8
A.2	Bivariate relationships between treatments colored by provenance (introduced / native). . . . .	8
C.1	Visualization of clustering assignments following K-medoids clustering. Non-metric multidimensional scaling (NMDS) ordination was conducted on all community observations from 2008 – 2018 (n=560). Pairwise community distance was calculated using Bray-Curtis dissimilarity index. Species vectors correspond to taxa that were found to be significantly associated ( $p < 0.05$ ) with state assignments using indicator species analysis. . . . .	15
C.2	Relative abundance of species across vegetation state assignments. Values refer to the average abundance of each species (+/- standard error) for observed communities assigned to each state. Species that served as significant ( $P < 0.05$ ) indicators of each state type are highlighted using “*” and colored by representative state. On average, indicator species of each vegetation state accounted for 75% of the cumulative relative abundance of observed communities. . . . .	16
C.3	Plot-level shifts in state assignment over time. For each observed community (grid cell), the state assignment of a community is presented as a function of initial seeding treatment (row) and time (column). . . . .	17



# Chapter 1

## UCD thesis fields

Placeholder

## Chapter 2

# The “Neutral Theory” of Niche Dimensionality

Placeholder

## Chapter 3

# Nitrogen enrichment has scale-dependent effects on plant diversity in California grasslands.

Evan E. Batzer<sup>1\*</sup> and Valerie T. Eviner<sup>1</sup>

1. Department of Plant Sciences, University of California, Davis

## Chapter 4

Climate drives transitions between  
vegetation states in California  
grasslands.

*ABSTRACT*

**Abstract**

**Introduction**

**Methods**

**Results**

**Discussion**

# Conclusion

If we don't want Conclusion to have a chapter number next to it, we can add the `{-}` attribute.

## More info

And here's some other random info: the first paragraph after a chapter title or section head *shouldn't be* indented, because indents are to tell the reader that you're starting a new paragraph. Since that's obvious after a chapter or section title, proper typesetting doesn't add an indent there.

# Appendix A

## Supporting information for Chapter 1

# APPENDIX A. SUPPORTING INFORMATION FOR CHAPTER 1

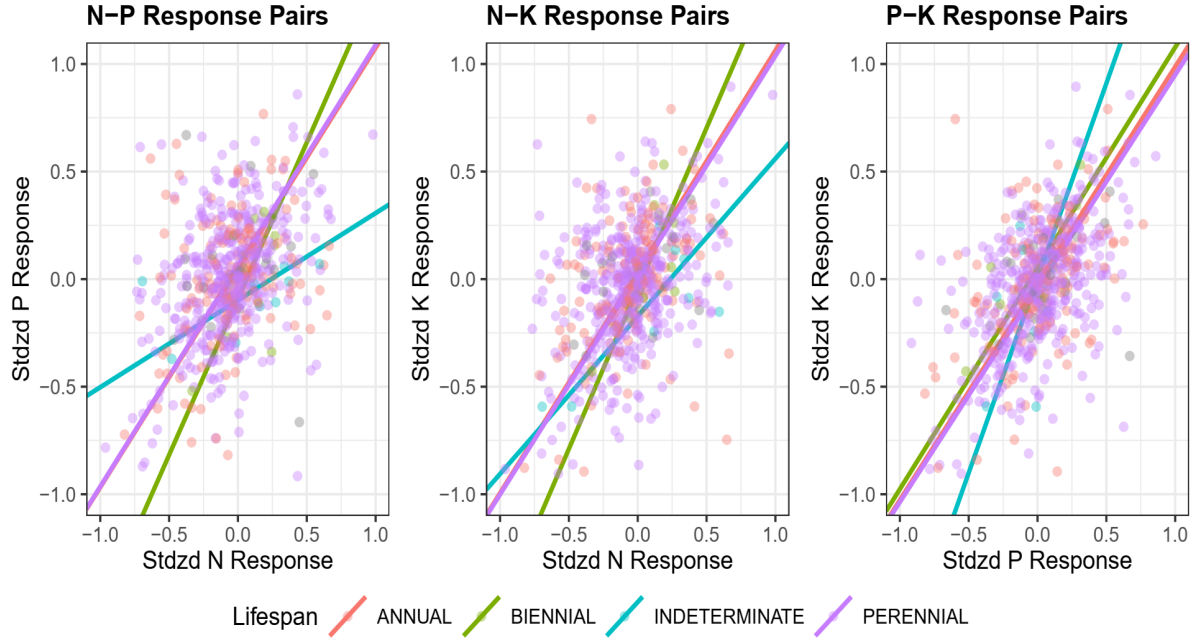


Figure A.1: Bivariate relationships between treatments colored by species lifespan.

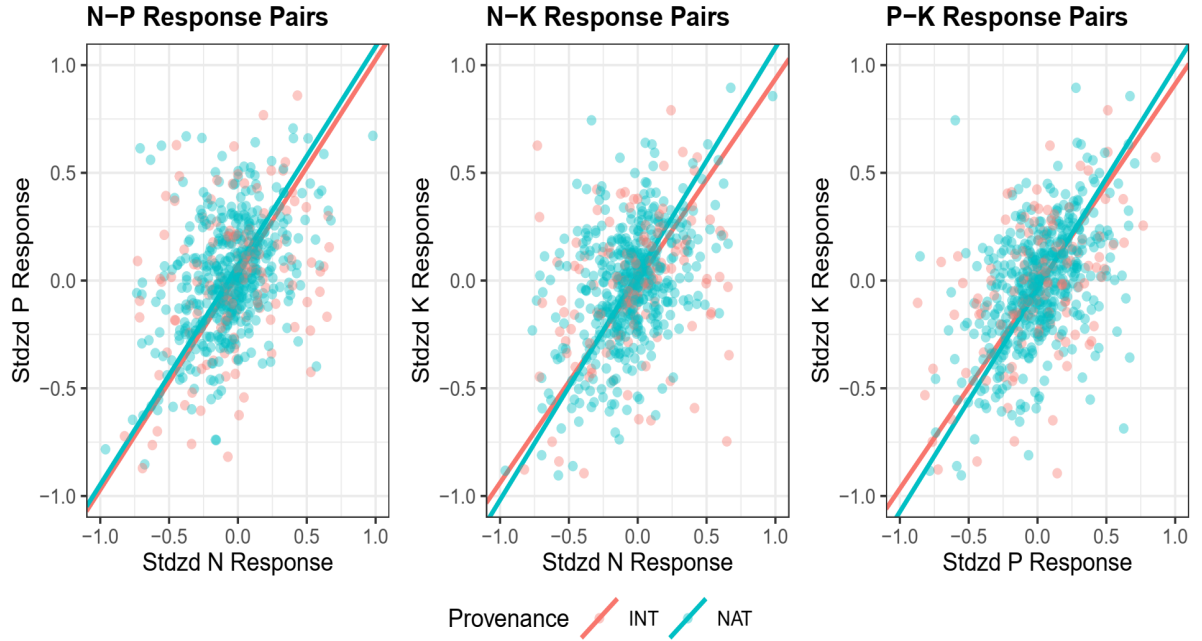


Figure A.2: Bivariate relationships between treatments colored by provenance (introduced / native).



Site Name	Continent	Country	Habitat	First Year	Last Year	Total Years	MAP	MAT	Taxa
Azi	Asia	CN	alpine grassland	2007	2012	5	711	1.36	43
Bogong	Australia	AU	alpine grassland	2009	2019	11	1678	5.98	19
Boulder South Campus	North America	US	shortgrass prairie	2008	2016	9	487	9.9	9
Bunchgrass (Andrews LTER)	North America	US	montane grassland	2007	2018	12	1618	6.77	10
Burrawan	Australia	AU	semiarid grassland	2008	2019	12	643	18.22	10
Cedar Creek LTER	North America	US	tallgrass prairie	2007	2018	12	740	6.34	8
Cedar Point Biological Station	North America	US	shortgrass prairie	2007	2019	13	456	9.64	12
CEREEP - Ecotron IDF	Europe	FR	old field	2012	2018	7	632	10.82	16
Chichaqua Bottoms	North America	US	tallgrass prairie	2009	2019	11	871	9.26	6
Companhia das Lezírias	Europe	PT	annual grassland	2012	2019	8	564	16.58	26
Cowichan	North America	CA	old field	2007	2018	12	762	10.45	5
Elliott Chaparral	North America	US	annual grassland	2008	2019	11	344	17.71	6
Ethabuka (Main Camp)	Australia	AU	desert grassland	2013	2019	7	192	24.06	4
Ethabuka (South Site)	Australia	AU	desert grassland	2013	2019	7	203	23.95	3
Fruebuel	Europe	CH	pasture	2008	2015	8	1546	6.96	15
Hall's Prairie	North America	US	tallgrass prairie	2007	2014	8	1289	13.83	4
Hart Mountain	North America	US	shrub steppe	2007	2012	6	259	7.75	11
Heronsbrook (Silwood Park)	Europe	UK	mesic grassland	2007	2013	7	668	10.17	19
Hopland REC	North America	US	annual grassland	2007	2019	13	1065	13.24	19
Jena	Europe	DE	grassland	2013	2018	6	654	8.57	18
Kibber (Spiti)	Asia	IN	alpine grassland	2011	2018	8	400	-1.45	7
Kilpisjärvi	Europe	FI	tundra grassland	2013	2018	6	569	-3.25	24
Kinypanial	Australia	AU	semiarid grassland	2007	2018	11	408	15.59	8
Koffler Scientific Reserve	North America	CA	pasture	2010	2019	10	853	6.28	10
Konza LTER	North America	US	tallgrass prairie	2007	2019	13	889	12.08	17
Lancaster	Europe	UK	mesic grassland	2008	2017	10	1522	8.01	10
Las Chilcas	South America	AR	mesic grassland	2013	2019	7	955	15.09	8
Lookout (Andrews LTER)	North America	US	montane grassland	2007	2018	12	1877	6.9	8
Mar Chiquita	South America	AR	grassland	2011	2018	8	907	14.32	14
McLaughlin UCNRS	North America	US	annual grassland	2007	2019	13	936	13.97	8
Mt. Caroline	Australia	AU	savanna	2008	2018	11	324	17.75	15
Pingelly Paddock	Australia	AU	old field	2013	2018	6	456	16.28	10
Pinjarra Hills	Australia	AU	pasture	2013	2018	5	1085	19.99	5
Rookery (Silwood Park)	Europe	UK	mesic grassland	2007	2013	7	685	10.13	12
Saana	Europe	FI	montane grassland	2014	2019	6	521	-2.6	25
Sagehen Creek UCNRS	North America	US	montane grassland	2007	2013	7	831	5.83	16
Savannah River	North America	US	savanna	2007	2012	6	1184	17.43	12
Sedgwick Reserve UCNRS	North America	US	annual grassland	2007	2017	11	478	15.58	4
Sevilleta LTER	North America	US	desert grassland	2007	2018	12	252	13.06	5
Sheep Experimental Station	North America	US	shrub steppe	2007	2016	10	246	5.32	18
Shortgrass Steppe LTER	North America	US	shortgrass prairie	2007	2018	12	369	8.95	6
Sierra Foothills REC	North America	US	annual grassland	2007	2019	13	936	16.31	7
Smith Prairie	North America	US	mesic grassland	2007	2016	10	605	10.18	25
Spindletop	North America	US	pasture	2007	2019	13	1152	12.48	9
Temple	North America	US	tallgrass prairie	2007	2016	10	877	19.4	15
Trelease	North America	US	tallgrass prairie	2008	2017	10	992	11.07	5
Ukulinga	Africa	ZA	mesic grassland	2009	2018	10	832	17.65	17
Val Mustair	Europe	CH	alpine grassland	2008	2019	11	681	0.13	30
Yarramundi	Australia	AU	mesic grassland	2014	2019	6	844	17.32	5

Table A.1: Table of sites included in analysis.

# APPENDIX A. SUPPORTING INFORMATION FOR CHAPTER 1

Site Name	$\rho(\text{N-P})$	$\rho(\text{N-K})$	$\rho(\text{P-K})$	$\Delta\text{N}$	$\Delta\text{P}$	$\Delta\text{K}$	D
Azi	0.4	0.68	0.47	1.3	1.35	1.44	0.32
Bogong	0.28	0.59	0.57	0.44*	0.42*	0.38*	0.35
Boulder South Campus	-0.06	0.05	0.67	0.44	0.56*	0.44	0.52
Bunchgrass (Andrews LTER)	0.22	0.67	0.52	0.25	0.46*	0.43*	0.35
Burrawan	0.26	0.32	-0.03	0.17	0.2	0.17	0.54
Cedar Creek LTER	0.43	0.14	0.57	0.53*	0.18	0.22	0.41
Cedar Point Biological Station	0.2	0.18	0.43	0.36*	0.23*	0.27*	0.49
CEREEP - Ecotron IDF	0.13	0.15	0.61	1.12*	0.91	1.12*	0.47
Chichaqua Bottoms	0.48	0.57	0.6	0.30*	0.25	0.27*	0.3
Companhia das Lezirias	0.44	0.2	0.38	1.15*	1.10*	0.75	0.44
Cowichan	-0.3	0.66	-0.01	0.12	0.27*	0.17	0.59
Elliott Chaparral	0.5	-0.12	0.66	0.22	0.26	0.27	0.44
Ethabuka (Main Camp)	-0.08	0.57	0.28	0.28	0.83*	0.43	0.5
Ethabuka (South Site)	0.77	0.88	0.92	0.59*	0.32	0.52	0.09
Fruebuel	0.58	0.15	0.49	1.05*	0.99*	0.83*	0.4
Hall's Prairie	0.56	0.58	0.04	1.13*	0.66*	0.68*	0.4
Hart Mountain	0.91	0.46	0.5	0.96*	0.73	0.57	0.25
Heronbrook (Silwood Park)	0.21	0.6	0.28	1.03*	0.67	0.66	0.42
Hopland REC	0.33	0.75	0.58	1.01*	0.49	0.68*	0.3
Jena	-0.25	0.06	0.2	0.97*	0.62	0.64	0.67
Kibber (Spiti)	0.3	0.48	0.74	0.25	0.26	0.27	0.33
Kilpisjärvi	0.4	0.22	0.8	1.03*	0.78	0.46	0.35
Kinypanial	-0.08	0.23	0.84	0.16	0.32	0.26	0.45
Koffler Scientific Reserve at Joker's Hill	0.32	0.6	0.53	0.88*	0.65*	0.54*	0.34
Konza LTER	0.29	0.23	0.55	0.43*	0.28	0.37	0.43
Lancaster	0.55	0.57	0.57	0.44	0.38	0.38	0.29
Las Chilcas	0.71	0.55	0.83	0.78*	0.52	0.84*	0.2
Lookout (Andrews LTER)	0.66	0.88	0.86	0.38*	0.39*	0.50*	0.13
Mar Chiquita	0.75	0.54	0.6	0.62	0.58	0.6	0.25
McLaughlin UCNRs	0.51	0.24	0.24	0.41	0.33	0.38	0.45
Mt. Caroline	0.67	0.71	0.6	0.67*	0.62*	0.52*	0.23
Pingelly Paddock	0.46	-0.08	-0.29	0.74	1.28*	0.61	0.65
Pinjarra Hills	0.55	0.25	0.81	0.78	1.06	0.77	0.31
Rookery (Silwood Park)	0.8	0.74	0.8	0.99*	1.50*	0.73	0.15
Saana	0.61	0.56	0.62	1.25*	0.98*	1.09*	0.27
Sagehen Creek UCNRs	0.12	0.49	0.17	0.63	0.49	0.45	0.49
Savannah River	0.42	0.12	0.38	0.76	0.99	0.55	0.46
Sedgwick Reserve UCNRs	0.61	0.84	0.94	0.38*	0.39*	0.36*	0.14
Sevilleta LTER	0.8	0.92	0.94	0.36*	0.14	0.14	0.08
Sheep Experimental Station	-0.11	0.53	-0.12	0.28*	0.17	0.21	0.6
Shortgrass Steppe LTER	-0.01	0.36	0.53	0.43*	0.26*	0.1	0.47
Sierra Foothills REC	-0.38	0.23	0.59	0.34	0.24	0.29	0.57
Smith Prairie	0.15	0.15	0.06	0.53*	0.47*	0.35	0.59
Spindletop	0.66	0.14	0.2	0.24	0.25	0.60*	0.44
Temple	0.28	0.24	0.5	0.41	0.61*	0.55	0.44
Trelease	-0.27	-0.51	0.48	0.55*	0.28	0.23	0.73
Ukulinga	0.17	-0.06	0.51	0.58*	0.51*	0.75*	0.53
Val Mustair	0.56	0.4	0.45	0.45*	0.57*	0.3	0.35
Yarramundi	0.75	0.65	0.2	0.36	0.36	0.65*	0.31

Table A.2: Table of sites, pairwise correlations between community responses to different treatments ( $\rho$ ), rate of community change in response to treatment ( $\Delta$ ), and estimated response dimensionality (D). Significant ( $P < 0.05$ ) magnitudes of community response are labelled with \*.

## Appendix B

### Supporting information for Chapter 2

# Appendix C

## Supporting information for Chapter 3

Source	DF	SS	MS	F	R-squared	P
Seeding composition	6	12.0487	2.0081	32.815	0.8	0.001
Residual	49	2.9986	0.19928			
Total	55	15.0473	1			

Table C.1: Heuristics used to determine best number of clusters to use in partitioning, K. Summary of the best performing K for 8 different clustering indices.

K	Hartigan	Rk	CH	Rk	Beale	Rk	KL	Rk	Cindex	Rk	DB	Rk	Sil.	Rk	Duda	Rk
2	133.88	9	163.1	3	2.7	8	1.22	5	0.5	9	1.69	9	0.21	9	0.82	9
3	128.56	5	166.15	2	1.96	7	1.12	6	0.45	8	1.59	8	0.23	8	0.86	7
4	52.25	1	176.75	1	-2.02	1	3.09	2	0.42	7	1.49	6	0.26	7	1.19	1
5	70	7	156.78	5	5.41	9	0.7	8	0.4	6	1.42	3	0.27	6	0.7	8
6	84.36	6	153.65	6	-2.03	2	0.87	7	0.36	4	1.48	5	0.3	2	1.2	3
7	28.88	2	159.7	4	1.12	6	3.83	1	0.36	5	1.4	1	0.3	1	0.92	6
8	63.54	8	147.31	9	-3.12	3	0.39	9	0.31	1	1.5	7	0.27	5	1.34	4
9	48.78	4	150.17	7	-2.06	5	1.42	4	0.33	3	1.47	4	0.29	3	1.2	5
10	25.57	3	149.47	8	-9.33	4	2.24	3	0.32	2	1.42	2	0.28	4	4.2	2

Table C.2: Rank summary table of performance across different clustering indices.

### Clustering Index Ranking Method:

1. Hartigan: Choose value  $K$  with maximum index difference between  $K$  and  $K-1$ .
2. CH: Choose maximum value among orders of  $K$  considered.
3. Beale: Choose minimum value of  $K$  such that the critical value of the index is less than  $\alpha = 0.05$ . Other values whose critical value is less than  $\alpha$  are ranked in order of significance.
4. KL: Choose maximum value among orders of  $K$  considered.
5. Cindex: Choose minimum value among orders of  $K$  considered.
6. DB (Davies and Bouldin): Choose minimum value among orders of  $K$  considered.
7. Silhouette: Choose maximum value among orders of  $K$  considered.
8. Duda: Choose minimum value of  $K$  such that the critical value of the index is less than  $\alpha = 0.05$ . Other values whose critical value is less than  $\alpha$  are ranked in order of significance.

### APPENDIX C. SUPPORTING INFORMATION FOR CHAPTER 3

	Native perennial	F. perennis - B.hordeaceous	Invasive Annual	A. fatua - B. diandrus
Native perennial	95	8	7	29
F. perennis - B.hordeaceous	10	50	30	29
Invasive Annual	25	11	115	22
A. fatua - B. diandrus	19	21	7	76

Table C.3: Contingency table of observed transitions between state assignments between 2008-2018. For each plot observation of a state assignment in year  $t$  (rows), data shows the frequency of state assignments (columns) of the same plot in a subsequent year ( $t + 1$ ). Diagonal values represent the frequency of a given state retaining its assignment (persistence), while off-diagonal values represent transitions in state assignment. Changes in assignment frequency were highly non-random ( $\chi^2 = 392.017$ ,  $df = 9$ ,  $P < 0.001$ ).

Model	DF	Priority	1 Year SPEI	2 Year SPEI	3 Year SPEI	deltaAIC	AIC
1	12					35.31	1289.98
2	24	X				6.16	1260.83
3	24		X			31.82	1286.49
4	24			X		31.76	1286.43
5	24				X	28.00	1282.67
6	36	X	X			0.00	1254.67
7	36	X		X		3.92	1258.59
8	36	X			X	0.25	1254.92

Table C.4: AIC model comparison used to select the best fit multi-state model from a series of candidates. Covariates include “Priority Effects” – the effect of initial seeding mixture representation of indicator species correlated with cluster assignments – and “1-“, “2-“, and “3-year SPEI” – a standardized measure of drought stress computed over 1, 2, and 3 cumulative water year intervals, respectively. DF corresponds to the number of parameters estimated within the transition matrix, including baseline transition probabilities and effects of covariates.

Year: 2008

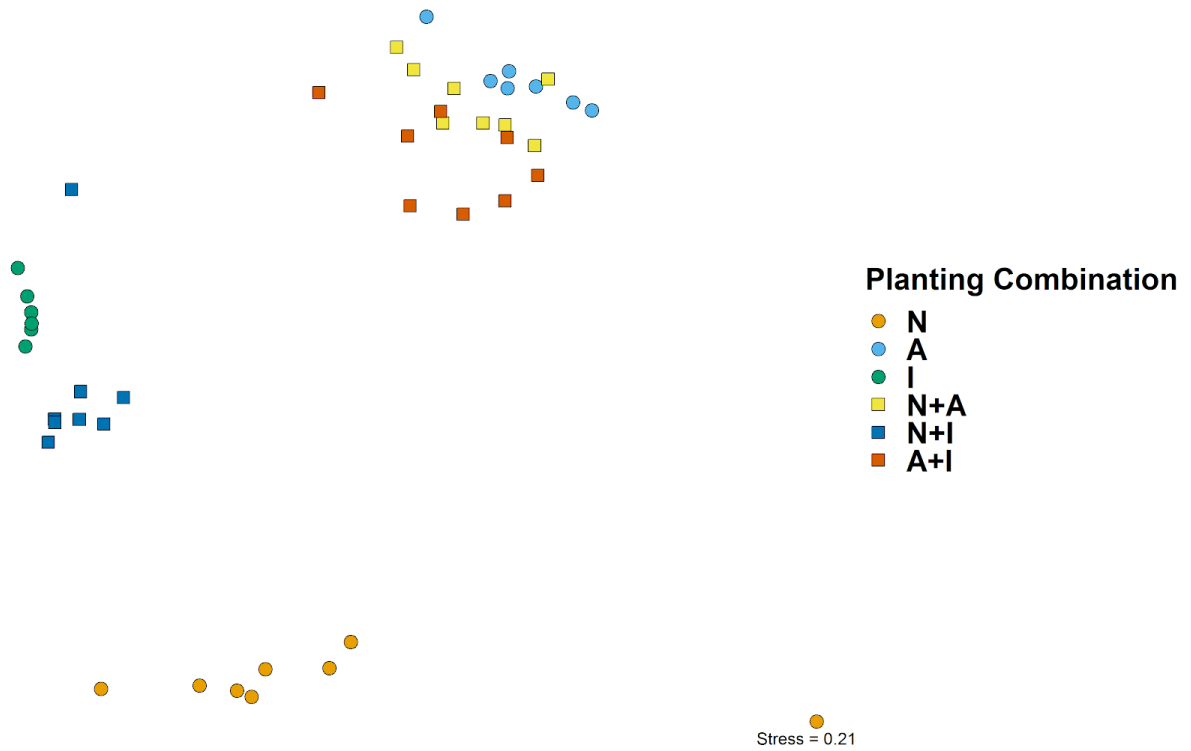


Figure C.1: Visualization of clustering assignments following K-medoids clustering. Non-metric multidimensional scaling (NMDS) ordination was conducted on all community observations from 2008 – 2018 ( $n=560$ ). Pairwise community distance was calculated using Bray-Curtis dissimilarity index. Species vectors correspond to taxa that were found to be significantly associated ( $p < 0.05$ ) with state assignments using indicator species analysis.

# APPENDIX C. SUPPORTING INFORMATION FOR CHAPTER 3

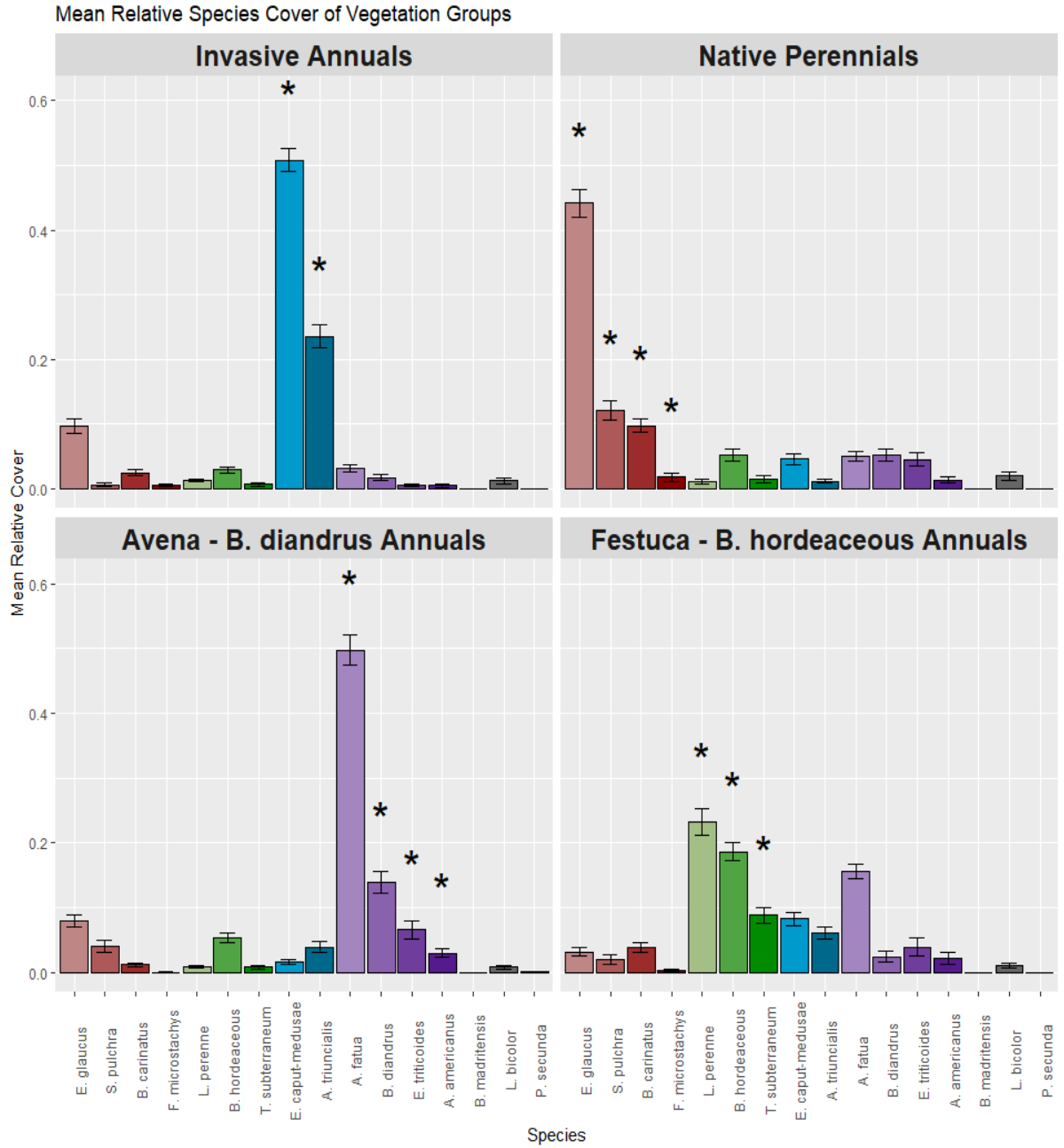


Figure C.2: Relative abundance of species across vegetation state assignments. Values refer to the average abundance of each species (+/- standard error) for observed communities assigned to each state. Species that served as significant ( $P < 0.05$ ) indicators of each state type are highlighted using “\*” and colored by representative state. On average, indicator species of each vegetation state accounted for 75% of the cumulative relative abundance of observed communities.



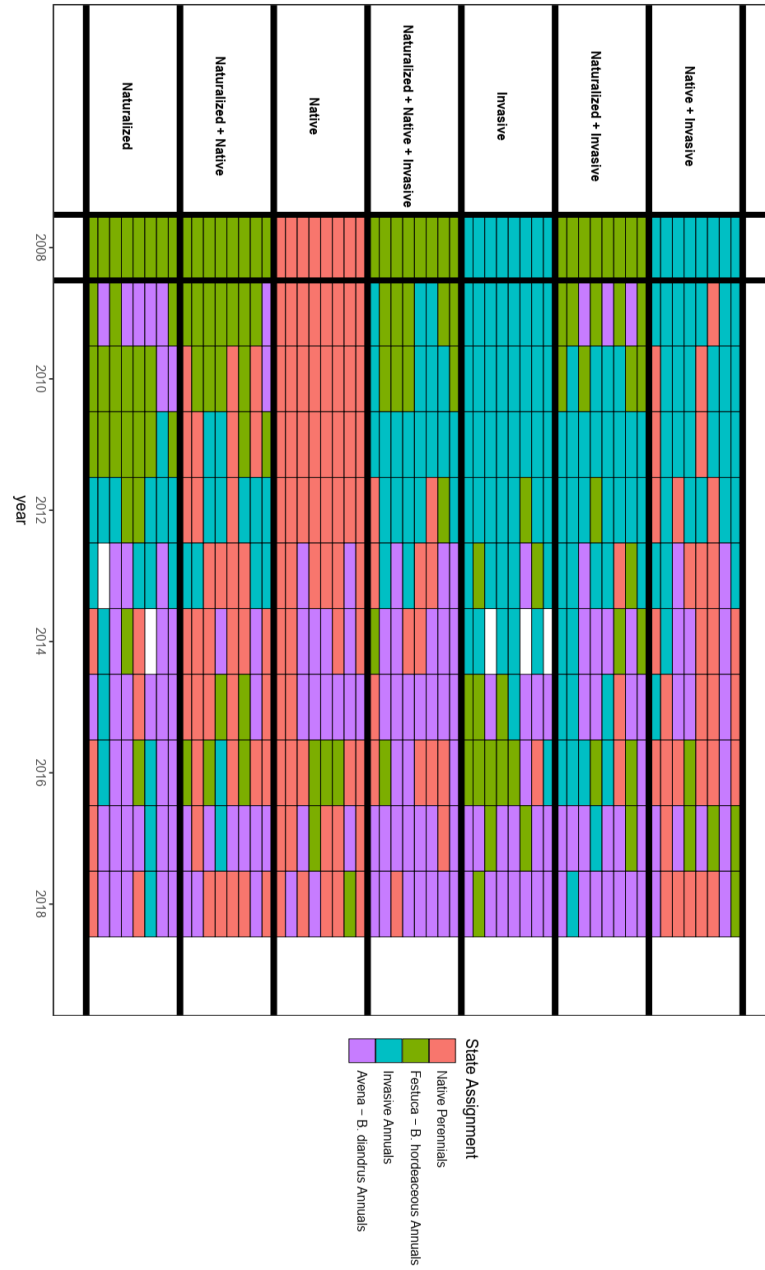


Figure C.3: Plot-level shifts in state assignment over time. For each observed community (grid cell), the state assignment of a community is presented as a function of initial seeding treatment (row) and time (column).

# References

Placeholder