

Environmental predictors of woody plant encroachment in calcareous fens are modified by biotic and abiotic land-use legacies

David Bart^{1*}, Tara Davenport² and Austin Yantes²

¹Department of Landscape Architecture and Nelson Institute for Environmental Studies, University of Wisconsin-Madison, 42 B Agricultural Hall, 1450 Linden Drive, Madison, WI 53706, USA; and ²Nelson Institute for Environmental Studies, University of Wisconsin-Madison, Madison, WI, USA

Summary

1. Woody plant encroachment in grasslands is a world-wide concern. Assertions that abiotic stress reduction facilitates encroachment are not universally supported. To devise restoration and management strategies, the ability of stress reduction, in the context of co-occurring biotic land-use legacies, needs to be assessed to predict shrub cover.

2. We determined whether legacy-induced reduction in *Carex stricta* (a potential facilitator of shrub encroachment and attractor of animal dispersers) and an increase in herbaceous invaders (potential competitors) altered the ability of stress reduction to predict woody plant cover in ploughed and never-ploughed plots within 11 Wisconsin (USA) calcareous fens. We hypothesized that drier conditions (low saturation stress) and higher nutrient availability associated with ploughing would be associated with high woody plant cover; that higher cover of herbaceous invaders associated with ploughing would predict low woody plant cover, and *C. stricta* cover predicts high woody plant cover in saturated, never-ploughed plots. Restricted maximum-likelihood (REML) multiple regression was used to determine the importance of interactions among ploughing, saturation, nutrients and the two biotic legacies in predicting woody richness and cover, as well as cover by dispersal syndromes and individual species.

3. Unexpectedly, encroachment by animal-dispersed species was higher in never-ploughed plots, while wind-dispersed species had no relationship with ploughing. Animal-dispersed species cover decreased with saturation stress in never-ploughed plots, only. *Carex* cover was associated with increased encroachment by animal-dispersed species, mainly in never-ploughed highly saturated plots. Herbaceous-invasive cover was associated with decreased encroachment. Wind-dispersed species cover declined with increasing saturation stress, with responses varying among species.

4. *Synthesis and applications.* The results suggest that the impacts of stress reduction on encroachment are not uniform and are modified by biotic legacies. We suggest that impacts of restoring stressful abiotic conditions on encroachment may not be known until the impacts on competitors and facilitators are understood.

Key-words: calcareous fens, land-use legacies, plant invasions, shrub encroachment, stress reduction, Wetlands

Introduction

Woody plant encroachment in graminoid-dominated systems is a global problem (Ratajczak, Nippert & Collins 2012; D'Odorico *et al.* 2013), reflecting the transition to

an alternative stable state (Brock & Carpenter 2010; Brandt *et al.* 2013). As such, encroachment can be very difficult to reverse (e.g. Sturm *et al.* 2005; Ratajczak *et al.* 2011). Encroachment is not well-studied in graminoid-dominated wetland systems, although the problem is known to occur (e.g. Curtis 1959; Middleton, Holsten & Diggelen 2006; Roberts, Kirkpatrick & McQuillan 2011).

*Correspondence author. E-mail: dbart@wisc.edu

Release from fire and grazing is broadly associated with woody plant encroachment world-wide (Van Auken 2000). However, spatial variations in encroachment after release suggest that some areas are more susceptible to encroachment than others (Ben Wu & Archer 2005; D'Odorico, Okin & Bestelmeyer 2012; Matson & Bart 2013). Why some areas remain resistant to encroachment after release is not well understood, particularly in wetlands. However, the ability to predict susceptibility to encroachment is critical for any attempt at restoring encroachment-resistant systems. In particular, this information would suggest whether some conditions preclude encroachment without reintroduction of burning or grazing regimes.

Proposed explanations for patterns of encroachment in high-stress systems (i.e. with abiotic factors that limit productivity (see Grime 1977), e.g. cold and wind (alpine), severe water limitation (deserts), low nutrient availability (alvars), root-zone anoxia (some wetlands)) include a combination of grazing/burning release and the alleviation of the main stressors (e.g. Ratajczak *et al.* 2011). In alpine and arctic systems, encroachment is often associated with warming (Brandt *et al.* 2013) and decreased snowpack (Aun, Hofgaard & Söderström 2011; Myers-Smith *et al.* 2011). In desert and semi-arid systems, changes in rainfall and decreased drainage (Ben Wu & Archer 2005) are associated with higher woody plant cover.

Similar interactions have long been invoked to account for patterns of encroachment in high-stress wetlands such as calcareous fens. In the mid-western USA, calcareous fens (hereinafter referred to as 'fens') are herbaceous systems where groundwater saturates close to the surface for most of the growing season and where carbon accumulates as histosols or tufa (Amon *et al.* 2002). Consistent saturation limits productivity in fens (Holte 1966) and is therefore considered the main stressor (*sensu* Grime 1977). As a result of consistent saturation stress, native floral diversity is often high (Amon *et al.* 2002), invasive richness low (Bart, Davenport & Carpenter 2015) and rare species richness very high compared to other systems (WDNR 2014).

Fens depend on fire or grazing to maintain an open, herbaceous species-dominated community (Curtis 1959; Middleton, Holsten & Diggelen 2006). In the absence of these activities, fens can quickly become invaded by successional woody species and ultimately transition to a shrub-carr. Although viewed as a natural process, this conversion is not a desirable management outcome (Wisconsin Department of Natural Resources (WDNR) 2014). Furthermore, once woody species are well-established, prescriptive burning may have little impact on cover, suggesting that the process is difficult to reverse.

Many studies have suggested that graminoid-dominated calcareous fens are more susceptible to woody plant encroachment when artificial drainage diminishes groundwater influence (Curtis 1959; Kogler & Howell 1981; Zimmerman 1983; Falb & Leopold 1993; Fojt & Harding

1995). In ploughed and drained fens, lower saturation stress (i.e. less consistent saturation of root zones) and increased nutrient availability persist after drainage features are rendered inoperable (Davenport, Bart & Carpenter 2014), suggesting that fens with a history of ploughing and drainage should be much more susceptible to encroachment. However, preliminary investigations suggest that both ploughed and unaltered fens are susceptible to encroachment (Bart, Davenport & Yantes 2013), and moreover, encroachment is patchy in all fens regardless of drainage or land-use history (unpublished data).

A possible reason for the patchiness is that stress alleviation may interact with biotic legacies (persistent population- or community-level changes resulting from abandoned land use, see Cramer, Hobbs & Standish 2008) resulting from the same land use that led to lower stress. In other systems, biotic legacies impact colonization by new species through a variety of mechanisms, including changes in dispersal vectors (Brown & Boutin 2009), introduction of highly competitive species (Kuhman, Pearson & Turner 2011) and the loss of facilitators (Gimeno *et al.* 2012). In ploughed and drained fens, there is a dramatic reduction in native graminoids (Davenport, Bart & Carpenter 2014), including the tussock-forming *Carex stricta* Lam. and a corresponding increase in competitive, herbaceous invaders (e.g. *Phalaris arundinacea* L., *Typha x glauca* Godr., *Ambrosia trifida* L., *Urtica dioica* L.). By increasing microtopographic heterogeneity, tussocks may provide critical refuges from high saturation stress, and therefore, facilitate establishment of species that otherwise would not survive (Vivian-Smith 1997; Crain & Bertness 2005). Tussocks are known to facilitate woody plant establishment in other wetland systems (Levine 2000; Stine, Resler & Campbell 2011). At the same time, increases in herbaceous-invasive cover associated with ploughing and drainage could also lead to pre-emption of or increased competition against woody species, especially under very low saturation stress where invasion by herbaceous species is most severe (Bart, Davenport & Carpenter 2015).

The loss of carices and simultaneous increase in herbaceous invaders may also limit encroachment by lowering habitat quality for dispersers. Many dispersers of *Cornus* spp., *Rhamnus cathartica* L. and *Frangula alnus* Mill. utilize *Carex* seed for food and tussocks for cover, while the seeds of many of the invaders are not particularly palatable (Illinois Wildflowers 2014). If this impacts encroachment, animal-dispersed woody species should be disproportionately affected by ploughing/drainage, *Carex* cover and invasive cover.

This study explores patterns of shrub encroachment within ploughed and never-ploughed Wisconsin (USA) calcareous fens to determine the importance of legacy stress reduction (lower saturation stress and higher nutrient availability) and biotic legacies (increased invasive species cover and loss of *Carex stricta*) in predicting encroachment. Specifically, we hypothesized:

1. Cover of woody plants will be higher in ploughed than never-ploughed plots. We expect this because of the generally lower saturation stress in ploughed plots, which has been implicated as a driver of woody plant encroachment in fens (Curtis 1959).

2. After accounting for saturation stress and nutrient availability (drivers of invasions by high biomass herbaceous-invasive species (Bart, Davenport & Carpenter 2015)), there should be a negative relationship between woody plant cover and herbaceous-invasive cover. We expect this negative relationship due to competition or pre-emption from the faster-growing herbaceous invaders.

3. After accounting for saturation stress, nutrient availability, and invasive cover, woody plant cover will increase with increasing *C. stricta* cover. We expect this positive relationship due to facilitation by *C. stricta* and the importance of carices as cover and forage for animal dispersers (Illinois Wildflowers 2014).

4. The impact of *Carex stricta* on shrub cover will be greater in ploughed plots than in never-ploughed plots. We expect this relationship because *C. stricta* is

ubiquitous in the absence of ploughing, while cover is much reduced when ploughed (Davenport, Bart & Carpenter 2014).

5. As saturation stress increases, the impacts of *Carex stricta* on woody plant cover will increase. We expect this association due to the facilitating effects of tussocks under anaerobic conditions (Crain & Bertness 2005).

6. High *Carex stricta* cover will predict high cover of animal-dispersed woody species, but not wind-dispersed woody species. We expect this because of the importance the plant has as cover and forage for dispersers.

Materials and methods

The study was conducted in 11 southern Wisconsin (WI) fen mounds (Fig. 1), including Wings over Wisconsin (WoW) A, B, D, and E (Medina), Cleman's Tract (Township of Oregon), Waterloo (Waterloo), Clover Valley A, B (Whitewater), Bluff Creek A and B (Whitewater) and Deansville Fen (Deansville). WoW B, D, E and Cleman's tract were completely ploughed at least once in the last 100 years. WoW A and Waterloo were both partially ploughed, and contain remnants of unaffected fen



Fig. 1. Study site locations in Wisconsin. Site names have been withheld from this figure due to their ecological sensitivity.

vegetation. The remainder was never ploughed. Although some fens were within the same management unit, each had distinct site and management histories (Table S1, Supporting Information) and formed distinct mounds. Although some fens were burned periodically, this has not had much impact on current woody plant cover (unpublished data; Matt Zine, WI DNR, personal communication). In all cases of ploughing except one (Cleman's Tract), artificial drainage was attempted. In all cases, drainage tiles and ditches no longer function, but the sites remain drier nonetheless (Davenport, Bart & Carpenter 2014). However, ploughed plots remained relatively wet, and never dried down to the point where water availability may become an issue (see Table S2 for a fen-level summary of hydrologic and nutrient measures). For the sake of simplicity, we refer to these fens or areas within fens as 'ploughed'. The soil for each fen is Houghton Muck (USDA NRCS 2013), although most never-ploughed fens contained hemic peat. Fen size ranged from 0.6 to 2.8 hectares. All fens have been managed as either natural areas or as potential restoration sites for at least 10 years.

Known history of grazing and burning is shown in Table S1. In all cases, significant periods (often a decade or more) of grazing and burning release have occurred, certainly sufficient to allow encroachment. Since the 1980s, controlled burns were initiated in several fens (Cleman's Tract, Bluff Creek A and B, Clover Valley A and B, Waterloo); however, burning has been sporadic, with sometimes a decade without burning (Brandt *et al.* 2013).

VEGETATION SAMPLING

We used a stratified random design, with 20 randomly established plots within each fen (220 plots total). Each plot consisted of a 1-m² plot (for herbaceous vegetation) nested within a 25-m² plot (for woody species). Herbaceous vegetation was surveyed in June and August of 2012. The cover of all herbaceous species was assessed on a log₂ scale (Gauch 1982). Woody plants were surveyed from August to October 2012. We established a 0.5-m grid in each 25-m² plot and used a point-intercept method at gridline intersections (100 points per plot) to determine percentage cover of each woody species.

HYDROLOGIC, NUTRIENT AND LAND-USE HISTORY MEASUREMENTS

Root-Zone Soil Volumetric Water Content (VWC) was measured in each plot every other week from May to October in 2012 (a drought year) and 2013 (an above average rainfall year) using a Decagon GS3 moisture sensor attached to a Decagon Pro-Check meter (Decagon Devices, Pulman Washington, USA). The following variables were measured: (i) maximum VWC, (ii) minimum VWC, (iii) mean VWC and (iv) range in VWC over the 2 year period.

Root-zone NH₄-N and NO₃-N was determined by KCl extraction in the University of Wisconsin Soil and Plant Analysis Lab (SPAL) (Bremner & Keeney 1965). Inorganic N was determined by summing both N species. Root-zone available P was determined using Bray's II sequential extraction at SPAL. Bray's II extraction (Bray & Kurtz 1945) was necessary due to the high pH and calcium content expected in fens. Methods for assessing plot-level plough history are described in Davenport, Bart & Carpenter (2014).

CREATION OF SATURATION STRESS AND NUTRIENT VARIABLES

For analyses, we sought to create one saturation stress and one nutrient variable to reduce dimensionality. All hydrologic and nutrient variables were centred and scaled by converting to Z-scores (SAS JMP v. 10). The saturation stress variable was created from VWC measures (max, min, mean and range of VWC) with principal component analysis (PCA, PC-Ord 6) using Euclidean distance measures. The first axis (Eigenvalue 3.374, 84.4% of variance explained) was positively associated with mean, minimum and maximum VWC, and negatively associated with range in VWC. The scores of this axis were our 'Saturation' (saturation stress) variable. Analysis of centred and scaled inorganic N and available P data revealed one significant axis (Eigenvalue 1.515, 75.77% of variance explained) which correlated with both inorganic N and available P. This axis was our 'Nutrient' variable.

CREATION OF VEGETATION CLASSES

Since we are concerned with woody plant encroachment, we limited our discussion to species not typically found in great numbers in healthy, well-managed systems. For this reason, woody species with affinities to Wisconsin calcareous fens (*Betula pumila* L., *Salix bebbiana* Sarg., *Salix candida* Flueggé ex Willd. and *Dasiphora fruticosa* (L.) Rydb) were not included in the analyses. The above-mentioned species rarely cause problems in fens (Matt Zine, Wisconsin Department of Natural Resources, Personal Communication) and are seldom associated with transitions to shrub-carr (unpublished data).

Total woody plant cover was assessed by counts of woody plant-occupied points in the 5 × 5 m plots. Cover by primarily animal-dispersed shrubs was determined by adding the number of points occupied by the following species: *Cornus sericea* L., *Cornus racemosa* Lam., *Frangula alnus*, *Rhamnus cathartica*, *Rubus* sp. and *Sambucus nigra* L.). Cover by primarily wind-dispersed woody species was determined by adding the number of points covered by *Populus tremuloides* Michx., *Salix discolor* Muhl., *Salix exigua* Nutt. and *Salix serissima* (L.H. Bailey) Fernald (see Table S3).

'Invasives' in this study were productive herbaceous species expanding their range into fens due to human activities. These included *Ambrosia trifida*, *Phalaris arundinacea*, *Phragmites australis*, *Typha x glauca* and *Urtica dioica*. Percentage cover of each invasive species was estimated as the midpoint in the range of each cover class (e.g. Cover Class 1 = 0.5%, Cover Class 2 = 1%, and so on). Cover for invasive species as a group in each subplot was then determined by adding the percentages of each species.

ANALYSES

Fens are among the rarest mid-western US systems (Eggers & Reed 1997), with fewer than 100 intact sites remaining in WI (Randy Hoffman, WDNR, personal communication), and known ploughed fens are even rarer. Because of the rarity of the system and our interest in within-fen susceptibility, we focused on plots within fens rather than differences among fens.

The impact of ploughing on plot-level woody species cover (as a whole, by dispersal syndrome, and for each species) was determined by residual maximum-likelihood (REML) ANOVA (JMP

Table 1. Restricted maximum-likelihood ANOVA results comparing richness and cover between never-ploughed and ploughed plots (ns = not significant, nm = no model due to failure of convergence)

Group/species	Never-ploughed (mean ± SE)	Ploughed (mean ± SE)	Variance component estimate (fen, residual)
Shrub richness	2.78 ± 0.29	1.82 ± 0.30	27.60, 72.40
	$F = 7.223, P = 0.0098$		
Shrub cover	48.04 ± 6.83	24.82 ± 7.06	22.78, 77.22
	$F = 7.8094, P = 0.0073$		
Animal-dispersed			
Group cover	24.56 ± 4.02	10.66 ± 4.17	20.14, 79.86
	$F = 7.6208, P = 0.0085$		
<i>Cornus racemosa</i>	5.16 ± 1.96	2.65 ± 2.03	18.57, 81.42
	ns		
<i>Cornus sericea</i>	18.67 ± 4.06	6.58 ± 4.17	29.58, 70.42
	$F = 6.8671, P = 0.0108$		
<i>Rhamnus cathartica</i>	0.67 ± 0.51	0.07 ± 0.53	6.00, 94.00
	ns		
<i>Frangula alnus</i>	1.84 ± 0.44	0.19 ± 0.46	5.22, 94.78
	$F = 7.0374, P = 0.0166$		
<i>Sambucus canadensis</i>	0.07 ± 0.21	0.59 ± 0.22	0.83, 99.17
	ns		
Wind-dispersed			
Group cover	23.28 ± 6.06	11.52 ± 6.21	37.83, 62.17
	ns		
<i>Populus tremuloides</i>	4.95 ± 3.32	4.51 ± 3.43	24.09, 75.01
	ns		
<i>Salix discolor</i>	2.80 ± 1.15	4.29 ± 1.20	4.13, 95.87
	nm		
<i>Salix exigua</i>	0.06 ± 0.32	0.82 ± 0.33	0, 100
	ns		
<i>Salix serissima</i>	0.31 ± 0.82	1.56 ± 0.85	17.48, 82.51
	ns		

11.0, SAS Institute Inc., Cary, North Carolina, USA)), with ploughing as a fixed effect and fen identity as a random effect. The residuals conformed to the assumptions of the model (see Kéry & Hatfield 2003), and data were left untransformed.

We assessed the importance of edaphic variables, ploughing, invasions and *Carex* cover on encroachment with REML multiple regression (JMP 11.0), with Saturation, Nutrients, *Carex*, Invasives and Ploughing as fixed effects and fen identity as a random effect. To assess whether ploughing altered the impact of the other predictor variables, we incorporated the interaction terms Saturation × Ploughed, Nutrients × Ploughed, *Carex* × Ploughed, and Invasives × Ploughed. To assess whether the impacts of *Carex* spp. cover on shrub encroachment depended on saturation stress, we included the interaction term *Carex* × Saturation. Separate models were run for diversity and cover for all woody plants, animal-dispersed species as a group, wind-dispersed species as a group, and each individual species. Only species found in more than three fens were included in the analysis. In each model, all variables were converted to Z scores to obtain standardized coefficients.

Results

Unexpectedly, woody plant richness and cover were significantly greater in never-ploughed than ploughed plots (Table 1). As a group, animal-dispersed woody plants had significantly higher cover in never-ploughed than ploughed plots, as did most of the animal-dispersed

species. However, only *Cornus sericea* and *Frangula alnus* were significant at a $P < 0.05$ level. There were no significant differences between ploughed and never-ploughed plots for any wind-dispersed species.

The results for the multivariate models (Table 2) suggest that woody plant cover and richness were negatively associated with invasive cover. Woody plant richness was positively associated with *Carex* spp. cover, but only in never-ploughed plots (Fig. 2a). As a group, animal-dispersed woody plant cover declined with increasing invasive cover and with high saturation stress in never-ploughed plots (Fig. 2b). However, animal-dispersed species cover increased with higher saturation stress when *Carex* spp. cover was high (Fig. 2c). *Cornus racemosa* cover was negatively associated with high saturation stress, high nutrient availability and high invasive cover, especially in never-ploughed plots (see Fig. S1, Supporting information). *Cornus sericea* was negatively associated with *Carex* spp. cover in never-ploughed plots and positively associated in ploughed plots and positively associated with *Carex* spp. cover under high saturation stress (Fig. 2d,e). *Frangula alnus* cover was positively associated with high saturation stress, but only in never-ploughed plots (Fig. S1). No significant models were produced for *Rhamnus cathartica* or *Sambucus nigra*.

Table 2. Restricted maximum-likelihood multiple regression results comparing richness and cover between never-ploughed and ploughed plots (RMSE = root mean square error). Only significant predictors and interactions are reported

Group/species	Coefficient	Fixed-effect estimates	Variance component estimate (fen, residual)
Shrub richness			
Ploughed (never-ploughed) × <i>Carex</i>	0.172	$F = 3.8373, P = 0.048$	
	$R^2 = 0.50, RMSE = 1.181, P < 0.0001$		26.27, 73.74
Shrub cover			
Invasive	-0.213	$F = 4.5792, P = 0.0355$	
	$R^2 = 0.35, RMSE = 30.99, P < 0.0001$		29.62, 70.38
Animal-dispersed			
Group cover			
Ploughed (never-ploughed) × Saturation	-0.226	$F = 4.6503, P = 0.0324$	
Invasive	-0.228	$F = 4.0746, P = 0.0449$	
<i>Carex</i> × Saturation	0.198	$F = 5.3394, P = 0.0220$	
	$R^2 = 0.35, RMSE = 20.18, P < 0.0001$		11.00, 89.00
<i>Cornus racemosa</i>			
Saturation	-0.441	$F = 22.7207, P < 0.0001$	
Nutrients	-0.382	$F = 9.2849, P = 0.0029$	
Ploughed (never-ploughed) × Saturation	-0.421	$F = 22.0562, P < 0.0001$	
Ploughed (never-ploughed) × Nutrients	-0.337	$F = 8.0621, P = 0.0051$	
Invasive	-0.259	$F = 7.0361, P = 0.0086$	
Ploughed (never-ploughed) × Invasive	-0.221	$F = 5.0921, P = 0.0251$	
	$R^2 = 0.38, RMSE = 9.02, P < 0.0001$		20.45, 79.55
<i>Cornus sericea</i>			
Ploughed (never-ploughed) × <i>Carex</i>	0.209	$F = 4.6560, P = 0.0328$	
<i>Carex</i> × Saturation	0.204	$F = 6.9743, P = 0.0089$	
	$R^2 = 0.38, RMSE = 16.49, P < 0.0001$		15.40, 84.60
<i>Frangula alnus</i>			
Ploughed (never-ploughed) × Sat	0.225	$F = 5.2247, P = 0.0232$	
	$R^2 = 0.20, RMSE = 3.24, P < 0.0001$		12.03, 87.97
Wind-dispersed			
Group cover			
Saturation	-0.197	$F = 4.5135, P = 0.0348$	
	$R^2 = 0.32, RMSE = 11.87, P < 0.0001$		53.81, 46.19
<i>Salix exigua</i>			
Saturation	-0.048	$F = 4.5531, P = 0.0346$	
	$R^2 = 0.13, RMSE = 3.47, P < 0.0001$		11.52, 88.48
<i>Salix discolor</i>			
<i>Carex</i>	0.258	$F = 7.1767, P = 0.0083$	
	$R^2 = 0.11, RMSE = 9.12, P < 0.0001$		4.66, 95.44
<i>Populus tremuloides</i>			
Saturation	-0.212	$F = 4.7056, P = 0.0312$	
	$R^2 = 0.30, RMSE = 14.66, P < 0.0001$		26.39, 73.61

As a group, wind-dispersed shrub cover was negatively associated with saturation stress, as were *Salix exigua* and *Populus tremuloides*. *Salix discolor* was positively associated with *Carex* spp. cover. No significant model was produced for *Salix serissima*.

Discussion

Contrary to expectations, our analyses suggest that drier conditions associated with ploughing did not uniformly predict shrub encroachment. Indeed, with some species drier conditions predicted lower cover. Our analyses also suggest the relationship between saturation stress and woody plant encroachment are, for some species, modified by biotic legacies (*Carex stricta* removal and increased cover of herbaceous invaders) brought about by

ploughing. Above all else, our findings suggest that there is no one clear set of drivers of woody encroachment, *per se*. Some shrubs encroach under drier conditions, while others may encroach under typical fen hydrologic conditions.

Our failure to support the hypotheses that woody plant encroachment would (i) be more common in ploughed fens and (ii) uniformly decrease with higher saturation stress is unexpected, because generally drier conditions associated with ploughing (Davenport, Bart & Carpenter 2014) would be expected to increase susceptibility (e.g. Kogler & Howell 1981). Rather, we found that increasing saturation stress predicted higher cover in several species in never-ploughed plots (e.g. *Frangula alnus*, *Cweornus sericea*) or when *C. stricta* cover was high (e.g. *Cornus sericea*). With other species, however, cover had a

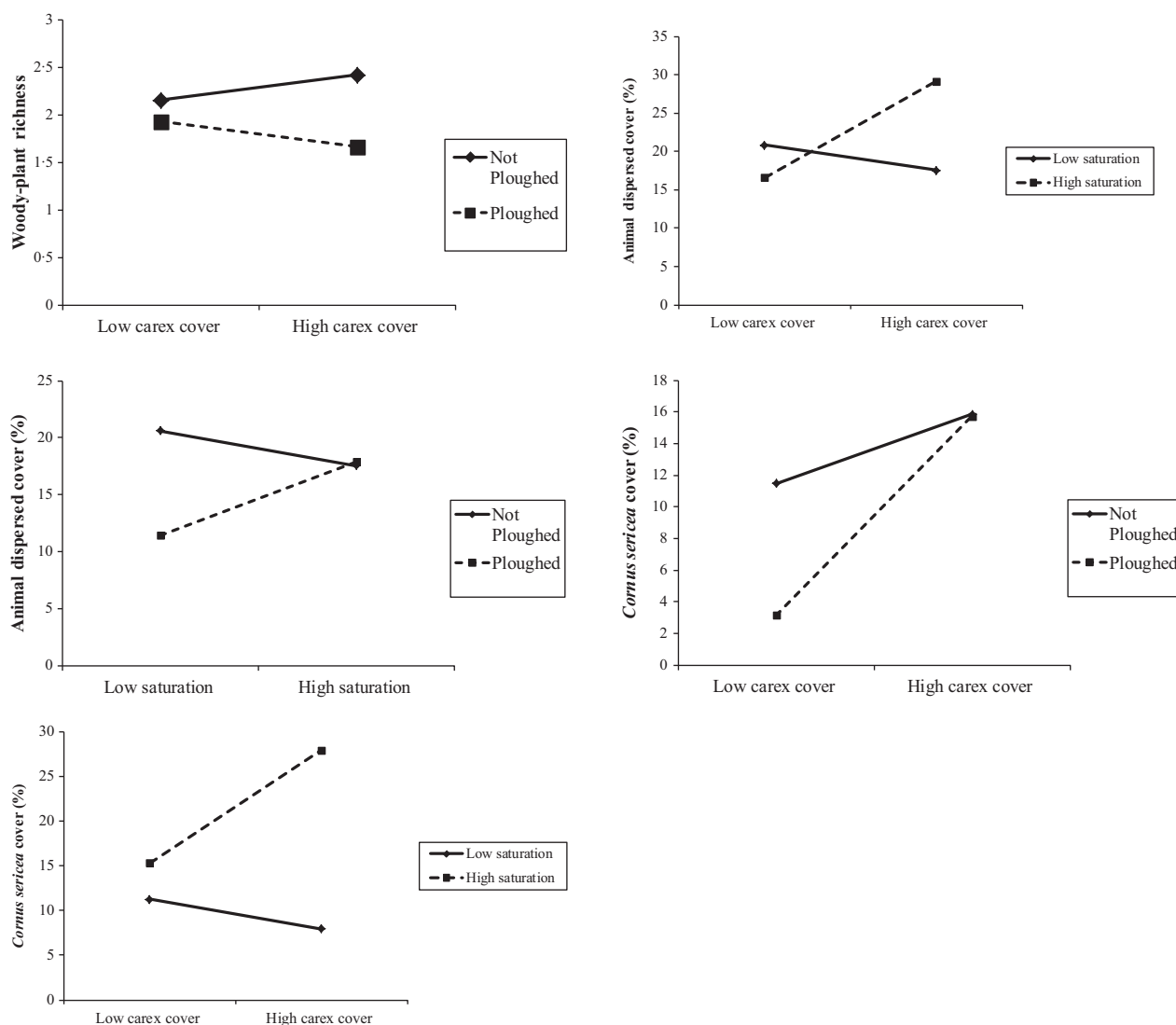


Fig. 2. Plots for significant interactions for select groups and species. See Fig. S1 for remaining interaction plots. 'High' and 'low' values for independent variables and continuous moderators are ± 1 STE.

negative association with saturation (e.g. *Cornus racemosa*, *Salix exigua*, *Populus tremuloides*). These data suggest that the responses to saturation stress are species-specific and might be mitigated, for some species, by *C. stricta* cover and plough history.

One of the consequences of diminished saturation stress in fens is increased cover of competitive invasive herbs (Bart, Davenport & Carpenter 2015). One possible explanation for our unexpected findings is that these invasions may be partially responsible for the more limited role of stress reduction in encroachment. Our failure to reject the hypothesis that higher invasive cover would predict lower woody plant cover as a whole as well as for some species (e.g. *Cornus racemosa*) lends some support to this assertion. Obvious mechanisms linking high invasive cover with lower levels of encroachment include pre-emption or competition between the more productive invasive herbs and the encroaching woody species. Competitive invaders, taking advantage of

decreased root-zone saturation and higher nutrient availability, would be at an advantage over the more stress-tolerant shrubs. Competition among invaders based on relative growth rates can be important in structuring communities (Kolb *et al.* 2002), and there is no reason to believe that under low stress competitive invaders could out-compete encroaching woody species.

Nevertheless, our findings that competitive invaders predominantly influenced animal-dispersed species suggest other important mechanisms. In particular, high cover of the competitive invaders in this study could lead to decreasing visitation by avian and mammalian dispersers. In our study, the competitive invaders either had tough seed coats (e.g. *Ambrosia trifida*), protective mechanisms (e.g. *Urtica dioica*) or had less palatable seeds (e.g. *Phalaris arundinacea*) than native graminoids (e.g. Illinois Wildflowers 2014). Whether or not this accounts for low shrub cover in highly invaded areas is unanswerable with these data, but it remains a possibility.

With shrub richness, animal-dispersed species cover and *Cornus sericea*, we failed to reject the hypothesis that increasing *C. stricta* cover predicts increasing woody plant cover. However, the significant *C. stricta* × ploughed and *C. stricta* × saturation interactions suggest that the association was strongest in wetter never-ploughed fens and that the biotic legacy of removing *C. stricta* from ploughed fens might in part be responsible for lower shrub cover in ploughed fens. *Carex* tussocks alleviate anoxic stress due to changes in microtopography (Crain & Bertness 2005) as well as the provision of stable substrates for germination and growth (Levine 2000). In other wetlands, encroachment is limited in permanently saturated substrates (Dunn & Sharitz 1987), and tussock formation can be positively associated with woody plant establishment (Stine, Resler & Campbell 2011). Thus, it is possible that the creation of an elevated and oxygenated tussock facilitates encroachment, especially under the most saturated conditions.

Contrary to our expectations, woody plant richness increased with increasing *Carex* cover in never-ploughed fens rather than ploughed fens. However, these findings are consistent with *Carex* facilitating some species by alleviating the higher saturation stress found in never-ploughed fens. It is possible that woody plant encroachment is subject to the 'Goldilocks Principle': at the high end of saturation stress, woody plants may not be able to establish without facilitative effects of *Carex* tussocks, which in turn are largely absent from most ploughed fens. At the low end of saturation stress seen in ploughed fens, the woody plants may simply be pre-empted or out-competed by herbaceous invaders.

The one exception seems to be *Frangula alnus*, which seems to have a strong positive relationship with saturation stress and is mostly present in never-ploughed plots. *F. alnus* is a non-native shrub that is well-adapted to hydrologic and edaphic conditions seen in mid-western fens (Converse 1984). Our findings reaffirm the assertion among managers (e.g. Wisconsin Department of Natural Resources (WDNR) 2014) that invasions by this shrub may be among the most difficult to prevent and manage in calcareous fens.

The impact of *Carex* cover seems to be greatest in primarily animal-dispersed species as a group. It is possible that *Carex* serves as an attractant to the mammals and birds which disperse these shrubs, although our data cannot definitively determine if this is the case. It should be known that various rodents hoard seeds (including *Cornus* spp.) in fen tussocks (Q. Carpenter, University of Wisconsin-Madison, personal communication).

Our findings suggest that saturated conditions should not be used to infer resistance to shrub encroachment in fens. Indeed, it seems that woody encroachment runs the gamut of saturation stress, with some species encroaching even under some of the wettest conditions. Furthermore, it seems that the impacts of drier conditions on encroachment cannot be predicted unless co-occurring biotic

legacies are taken into account. The fact that two of these legacies (decreased *Carex* and increased herbaceous-invasive cover) are important predictors of encroachment and can modify the impact of changes in hydrology has very real management implications. For example, management against woody plant encroachment might include hydrologic restoration, with hopes that increased saturation stress will increase encroachment resistance. Our data do indeed suggest that cover of some species declines with saturation stress, but only in unaltered fens and, with some species, when *Carex* cover is low. Hydrologic restoration in ploughed fens, therefore, may actually increase susceptibility to encroachment by some species if, as is usually desired, the new hydrology leads to a decline in herbaceous invaders and a return of carices.

Our data also reinforce claims made elsewhere (e.g. Ehrenfeld 2008) that creating conditions that resist invasions (*sensu lato*) by some species could inadvertently increase susceptibility to others. If cover by herbaceous invaders does indeed have a negative impact on encroachment, managers would do well to plan for increased cover of some woody plants after herbaceous invader cover is reduced and *Carex* cover is increased.

Finally, these results concur with previous studies (e.g. Middleton 2013) that prescriptive grazing or burning is the most important provider of resistance to encroachment in fens. Our data suggest only a subsidiary role of saturation: while an important constraint on encroachment by some species, with others saturated root zones seem to allow or even promote establishment. Since restoring a *Carex*-dominated system is probably among the restoration goals for many fens, the only recourse may be to manage encroachment through continued prescriptive measures.

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Data accessibility

Edaphic, hydrologic and species data: Dryad Digital Repository doi: 10.5061/dryad.6kg6c (Bart, Davenport & Yantes 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Land use and management summaries for study sites.

Table S2. Fen-level hydrologic and edaphic summaries.

Table S3. Woody plant species and dispersal syndromes.

Figure S1. Additional interaction plots.