Oikos 000: 001–008, 2012
doi: 10.1111/j.1600-0706.2012.20951.x

Subject Editor: James Bullock. Accepted 8 May 2012

Using structural equation modelling to test the passenger, driver and opportunist concepts in a *Poa pratensis* invasion

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The passenger, driver, and opportunist models are conceptual models of the invasion process used to describe alternative invasion scenarios. In the passenger model, both the invasive species and native community respond independently to environmental changes. In the driver model, changes to the native community are driven by the invasive species, while in the opportunist model invasion occurs in response to changes in the native community. In any given invasion scenario, however, it is possible that the relationships between the invasive, the native community, and the environment correspond to some combination of these invasion models acting simultaneously. We study invasion by *Poa pratensis* in a grassland in Alberta, Canada. *Poa pratensis* is a non-native plant implicated with loss of plant diversity in the region. In a three year field experiment, we manipulate the environment though defoliation, water addition, and nitrogen addition, and measure responses of *P. pratensis* cover, and cover and richness of the native community. We use structural equation modelling to describe the relationships between the invasive, the native community, and the environmental changes, and then interpret these relationships using the three invasion models. We found that *P. pratensis* predominantly invaded via the driver model, with subsequent reductions in native plant cover, but not in species richness. Positive effects of the environmental changes on *P. pratensis* also aided its ability to drive native cover. As well, we found some involvement of the opportunist model, through a negative relationship between the native community and the invasive. As invasion mainly proceeded via the driver model, management actions to limit invasion should focus on efforts to control abundance of *P. pratensis* itself.

Management programs for invasive plant species are often initiated based primarily on a species' non-native status, rather than on established effects on their new ecosystems (Davis et al. 2011). Considering the financial costs and ecological risks associated with invasive plant control, there has been a call for increased documentation of negative effects of invasive species prior to implementing extensive management plans (Davis et al. 2011). However, even when negative changes to the native community are concomitant with the introduction of a species, cause cannot always be attributed to the invasive.

Species rarely invade without concurrent environmental changes (Gurevitch and Padilla 2004), and thus invasive species can be mere passengers (Fig. 1a) increasing in abundance in response to concurrent and independent environmental changes, rather than true drivers of community change (Fig. 1b) (MacDougall and Turkington 2005). As another alternative model of invasion, the invasive may be an opportunist (Fig. 1c) increasing in response to otherwise unrelated changes to the native community (Chabrerie et al. 2008). This has major implications for management; if changes to the community do not originate with the invasive, control of the invasive is unlikely to promote plant community diversity, and efforts should focus instead on addressing the environmental or community changes at the root of the invasion.

These ideas have been discussed extensively in the literature as the passenger, driver and opportunist models of plant invasion (Didham et al. 2005, Chabrerie et al. 2008). These models provide a summary of complicated networks of interactions between the invasive species, the native community, and environment. There is, however, a myriad of interactions which can occur during the invasion process. Indeed, the original passenger/driver model proposed by MacDougall and Turkington (2005) has been expanded over time, first to include the opportunist model (Chabrerie et al. 2008) and, more recently, the back-seat driver model (Bauer 2012), which incorporates aspects of both passenger and driver models in addition to a temporal component. Also, there may be co-occurring relationships that provide simultaneous support for multiple invasion models; a recurring caveat is that in any given invasion

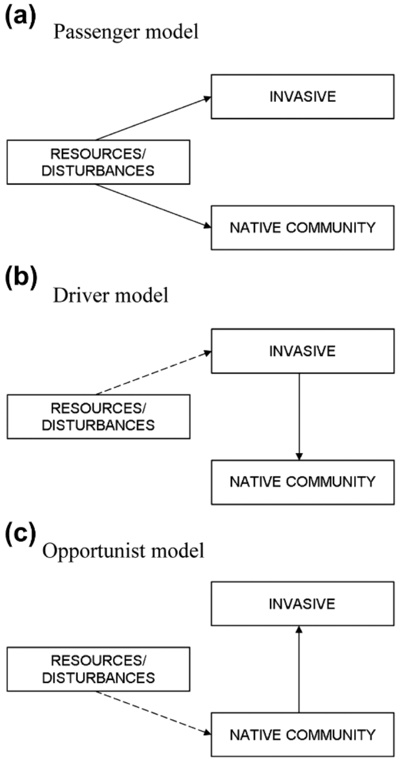

Figure 1. Adapted from Chabrerie et al. 2008. Three models of the links between the invasive species, the native community, and resources/disturbance through the invasion process: (a) passenger model: resources/disturbance impact both the invasive species and the community, simultaneously and independently; (b) driver model: the invasive species causes change to the native community; and (c) opportunist model: changes in the native community facilitate invasion. Solid arrows represent direct paths and dashed arrows indicate the indirect, optional involvement of resources/disturbance in the driver and opportunist models.

scenario, processes corresponding to a number of invasion models are likely operating simultaneously to different extents (Didham et al. 2005, MacDougall and Turkington 2005, Chabrerie et al. 2008). This is especially true following the establishment of the invasive species, as ecological and evolutionary circumstances permitting the initial invasion can change as the invasion proceeds (Dietz and Edwards 2006). Thus, rather than testing categorically for pre-defined conceptual models, we need a framework that focuses on the interactions between the players in the invasion process, and then uses the models to interpret these interactions.

The aim of the study was to use the three conceptual models to explain the relationships between an invasive species, the native plant community, and environmental changes. We assessed these relationships during three years of grassland invasion by *Poa pratensis* (Kentucky bluegrass) under manipulated resource and disturbance treatments, and then attributed these relationships to the established models of invasion. *Poa pratensis* is implicated with loss of plant diversity (Sather 1996), but the actual cause underlying this pattern of invasion remains unknown. For example, due to its strongly rhizomatous growth form, *P. pratensis* forms continuous stands able to outcompete native bunchgrasses (Grilz and Romo 1995), suggesting its mechanism of invasion corresponds to the driver model. However, there is evidence that the passenger model, through environmental changes such as grazing or altered resource levels, may also explain success of this invader. Overgrazing can increase *P. pratensis* abundance (Bailey et al. 2010) and is thought to promote *P. pratensis* invasion (Weaver 1954, Wroe et al. 2002), and increased resource levels are generally thought to increase invasibility of an ecosystem (Alpert et al. 2000, Davis et al. 2000).

The passenger, driver, and opportunist models represent three narratives of the complicated interactions between the invasive species, the native community, and the environment. However, an accurate examination of the invasion process needs to take a system-based approach that can qualitatively and quantitatively describe the many possible paths between variables involved in the invasion process. Then this complexity can be interpreted through an ecological framework, and attributed to one – or perhaps multiple – invasion models. As our statistical model, we use structural equation modelling, a type of path modelling, to evaluate the relationships between the invasive species, the native plant community, and environmental changes over three years. It is well-suited to the aims of our study, as it allows the evaluation of indirect and direct causal relationships, and of multiple simultaneous influences on a network of relationships (Grace 2006). Traditional univariate methods, which focus on one or at most a few processes at a time, and multivariate methods, which focus on net effects, lack the ability to evaluate these networks.

Methods

Study site

The study was conducted at a grassland site in the Foothills Fescue natural sub-region of southwest Alberta, Canada (51°14′42.02″N, 114°31′9.85″W). The area has a continental climate with average annual temperature of 4.1°C and precipitation of 413 mm, and average growing season (May–September) temperature of 13.2°C and precipitation of 313 mm (1971–2000 means, Environment Canada 2011). The study site was situated on a well-drained, west-facing upper terrace on Orthic Black Chernozem (Series: Dunvargan/Hatfield) soils (Soil Classification Working Group 1998). Historically, the site was moderately grazed (0.6 animal unit months ha^{-1}) by cattle, but this practice was ceased for the duration of the experiment. The site consists of approximately 60% cover of the dominant grass *Festuca campestris* and 7% cover of *Poa pratensis* on average, The remaining plant composition includes native graminoids, forbs, and shrubs, the most common plants being *Symphoricarpos occidentalis*, *Carex pensylvanica*, *Thermopsis rhombifolia*, *Achillea millefolium* and *Solidago missouriensis.*

Poa pratensis is a perennial, C3 grass that has invaded North American grasslands after being widely planted for lawns, pastures, and erosion control over the last century (Grace et al. 2001). It is generally considered to be of Eurasian origin, although it may be native to some parts of North America (Sather 1996). Nomenclature follows US Dept of Agriculture (USDA) PLANTS Database (2012).

In order to identify the dominant relationships responsible for invasion in this system, we tracked changes in *P. pratensis* and the native plant community over three years in response to experimentally-altered environmental conditions (altered resource levels and disturbance). In contrast to experimental designs that artificially manipulate invasive species abundance, this experiment attempted to simulate the conditions by which invasion might proceed in the field. We initiated a manipulative field experiment in November 2005, adding nitrogen and water, and simulating disturbance (summer and winter defoliation treatments, as a proxy for grazing), with all corresponding controls. We used a randomized, incomplete factorial design; all combinations of water addition and nitrogen addition were assessed with summer defoliation and winter defoliation, but summer defoliation and winter defoliation were not jointly assessed. Each of the twelve treatment combinations were replicated eight times. There were a total of 96 plots, each 1.5 × 1.5 m in size and arranged in a grid at a minimum distance of 0.25 m from the next plot. Defoliation was applied to the entire plot, while nitrogen and water were applied to a smaller 1 m by 1 m nested plot, and vegetation sampling occurred only within a central 50 × 50 cm sub-plot. Edges were mowed around the larger plot to further prevent edge effects.

Defoliation was applied once in either November 2005 or July 2006 to 1 cm height, consistent with winter (dormant season) and summer grazing in the region, respectively, and was accompanied by an undefoliated control. Nitrogen addition plots received granular urea (NPK: 46-0-0) in May of each year, with control plots receiving no fertilizer. Rates of urea addition were 10 g m^{-2} in 2006; due to the observed elevated nitrogen levels, addition was reduced to 5 g m^{-2} in 2007 and 2008. Plots received either ambient water (controls), or the water necessary to reach field capacity (added water treatment) every two weeks from 1 May to 31 August of each year (2006 through 2008). The amount of water added was determined using a moisture probe (Delta-T tm ML2C), coupled with calibrated relationships between water addition and observed measures of moisture for soil conditions at the site.

Sampling

We visually estimated the cover of vascular plant species, as percent cover by species, at peak growth in early August of each year in the 50 × 50 cm sampling plot. Cover values also included estimates of bare ground, moss and lichen, and litter cover. Cover data were used to obtain *P. pratensis* cover, native (i.e. non-*P. pratensis*) cover, and native species richness (number of species per 0.25 m^2, excluding *P. pratensis*). Native cover included low amounts of *Bromus inermis* ($< 2\%$), another non-native grass, which was too sparse to analyze separately, with the balance of vegetation comprised of native species. Biomass sampling was conducted at final sampling in August 2008, when all vegetation was clipped from the sampling plot, *P. pratensis* was sorted from native plants, and subsequently dried and weighed.

Volumetric soil moisture was sampled approximately every two weeks from May to September, from four random locations in each plot using a soil moisture probe (Delta-T tm ML2C). Soil nitrogen was measured using three soil samples, each 2.5 cm in diameter and 15 cm in depth, taken from each plot in August of each year (except for 2006, when only a subsample of plots were assessed). Samples were analyzed for available NO_3-N and NH_4-N by spectral absorption after extraction from soil using a 5:1 mixture of 2M KCl (Maynard and Kalre 1993).

Statistical analysis

We developed a structural equation model (SEM) based on hypothesized causal relationships from the resource addition (nitrogen and water) and disturbance (summer and winter defoliation) treatments, to the quantitative response variables *P. pratensis* percent cover (hereafter referred to as '*Poa*'), native plant percent cover ('cover'), and native species richness ('richness') (Fig. 2a). In addition to relationships from the resource/disturbance treatments to the response variables, the initial conceptual model explored all possible paths among response variables, expanded over the three years (Fig. 2b). This includes the effects within a single type of response variable (i.e. from *Poa* 2006 to *Poa* 2007), which we call 'residency effects'. We also considered relationships between native plant cover and richness as residency effects, as both are components of the native community. The model hypothesized that the response variables *Poa*, cover, and richness are controlled by resources and disturbance, as well as previous years' values of *Poa*, cover, and richness.

To statistically model change over time, we tested paths from the previous years' predictor variable and the current year's dependent variable. We chose to include plant cover rather than biomass in our SEM, as our annual cover measures enabled us to model change over time, while biomass was only sampled in the final year. We used an observed-variable SEM (i.e. without any latent variables) to assess the strength of both direct and indirect paths (Grace 2006). The strengths of indirect paths between response variables were quantified following path rules (Grace 2006). We also modelled covariance among those variables expected to co-vary (Fig. 2b). See Supplementary material Appendix A1 for more details on SEM methods.

To facilitate comparison among paths, we interpreted standardized paths, which are unitless and range from 0 to 1, rather than unstandardized paths (see Table A1 for full table of standardized and unstandardized paths). We included only statistically significant ($p \leq 0.05$) direct path and indirect paths over 0.10 standardized units in our interpretation, as the remainder of paths had negligible contribution to the SEM.

Interpretation

To interpret the relationships in the SEM, we determined whether each direct or indirect path corresponded to the passenger, driver, or opportunist models, or residency effect (Table 1). For this, we used response variables from only 2007 and 2008, as 2006 response variables are indicated by the resources/defoliation treatments only. Residency effects were those paths within a single type of response

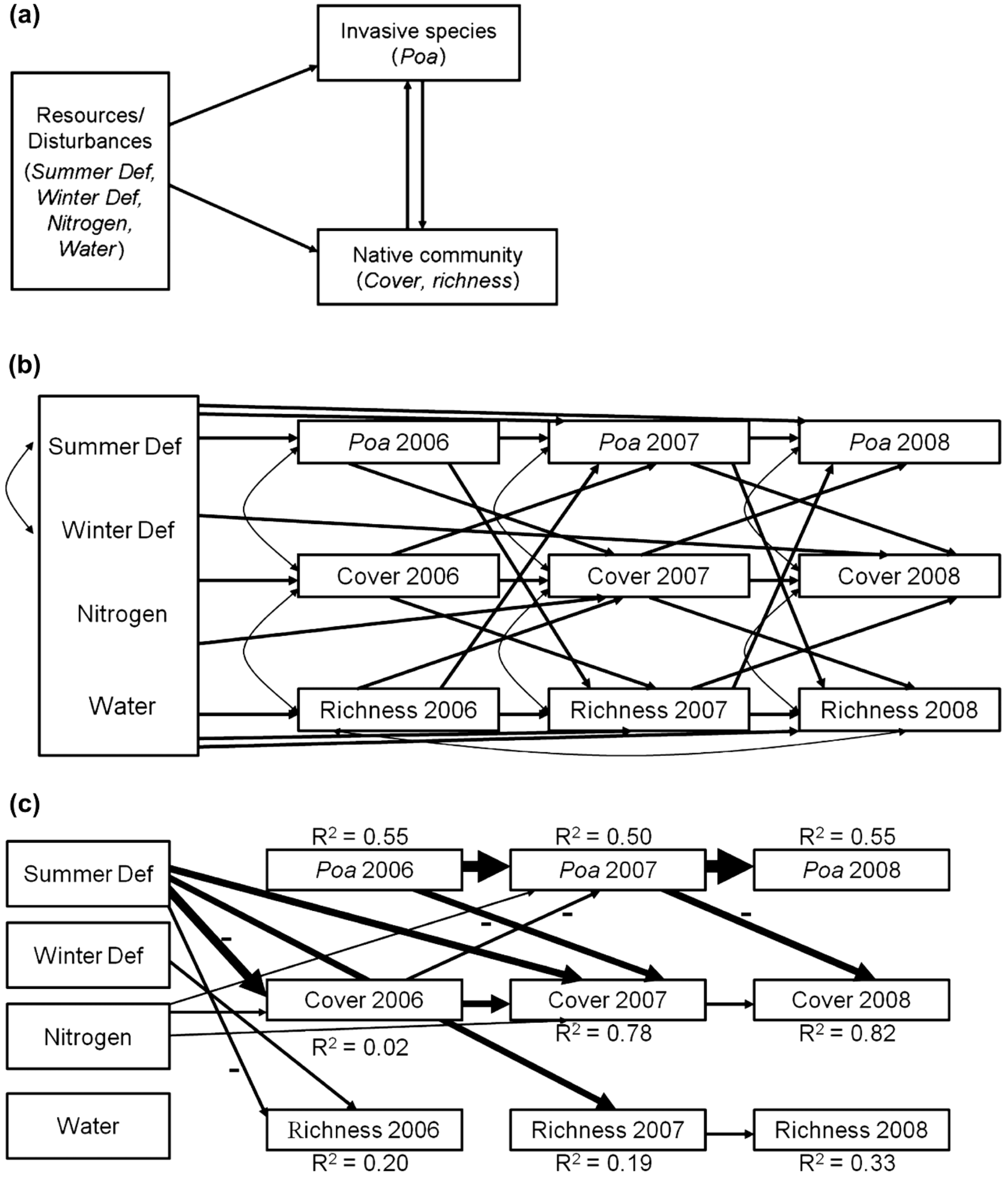

Figure 2. (a) Conceptual diagram linking the models developed by Chabrerie et al. 2008, depicted in Fig. 1, to our model (Fig. 2b) of the effects of resources/disturbance on *P. pratensis* cover, native cover, and native species richness over three years. This diagram specifies (in italics) our experimental variables in relation to the conceptual variables in Fig. 1, and includes all possible relationships between experimental variables. Our model (Fig. 2b) expands and tests these relationships over three years, and treats cover and richness as separate variables. (b) Initial model of the effect of resources/disturbance on the relationships between *P. pratensis* cover, native species cover, and native species richness over three years. The model depicts direct, causal relationships among variables (straight lines) and covariances among variables (curved lines). For simplicity in illustration, arrows from the resource/disturbance treatments to response variables are shown only once, although the model has paths from the four treatment variables to all response variables, as suggested in Fig. 2c. (c) Significant ($p \leq 0.05$) paths in final model. Arrow width corresponds to strength of standardized SEM coefficients, and '-' indicates the relationship is negative. The R^2-values represent the proportion of variance explained for each dependent variable.

variable, and between native plant cover and richness (Table 1). For the response variables cover and richness, any paths involving *Poa* as an intermediary were attributed to the driver model (Fig. 1). To be consistent with the passenger model, the environment must have a negative effect on the native community, as invasion is normally associated with degradation of the native community. Thus, all negative paths directly from the resource/disturbance treatments to cover or richness were attributed to the passenger model (Fig. 1). Likewise, for *Poa*, positive paths directly from the resource/disturbance treatments were attributed to the passenger model, and paths involving either cover or richness were attributed to the opportunist model. We summed values of all paths corresponding to each of the three conceptual models or residency effect for each response variable, and then calculated relative percent variance explained for each response variable by each of the three conceptual models or residency effect (Table 2).

Table 1. Standardized path coefficients for each of the statistically significant ($p \leq 0.05$) direct paths, and indirect paths over 0.10 standardized units, in our final model. Paths described end in the response variable indicated by column heading. Paths are coded as to whether they are indicative of the passenger (P), driver (D), or opportunist (O) model. Paths attributable to the residence effect of the previous years' community properties or *P. pratensis* abundance on current year's values are coded (R). One path (Cover 2006 → *Poa* 2007 → Cover 2008) cannot be identified with a singular model and is thus labeled "N/A".

Cover				Richness				*Poa*			
2007		2008		2007		2008		2007		2008	
Summer def (0.53)	P	*Poa* 2007 (−0.52)	D	Summer def (0.48)	P	Richness 2007 (0.27)	R	*Poa* 2006 (0.80)	R	*Poa* 2007 (0.91)	R
Cover 2006 (0.50)	R	*Poa* 2006 → *Poa* 2007 (−0.42)	D			Summer def → Richness 2007 (0.13)	P	Cover 2006 (−0.26)	O	Cover 2006 → *Poa* 2007 (−0.21)	O
Poa 2006 (−0.46)	D	Cover 2007 (0.25)	R					Summer def → Cover 2006 (0.17)	O	Summer def → Cover 2006 → *Poa* 2007 (0.15)	O
Summer def → Cover 2006 (−0.33)	P	Cover 2006 → *Poa* 2007 (0.14)	N/A					Nitrogen (0.12)	P	Nitrogen → *Poa* 2007 (0.11)	P
Nitrogen → Cover 2006 (0.10)	P	Summer def → Cover 2007 (0.13)	P								
		Cover 2006 → Cover 2007 (0.13)	R								
		Poa 2006 → Cover 2007 (−0.11)	D								

Table 2. Table of variance explained (%) by each of the passenger, driver, and opportunist models for each of the 2007 and 2008 native plant cover, species richness, and *Poa* cover variables. To calculate variance explained, we summed the values of all the paths corresponding to each of the three models for each response variable, and then calculated percent variance explained for each response variable by each of the three models, retaining sign to indicate whether the net effect was positive or negative. We also calculated what percent variance explained is attributable to the residence effect of the previous years' response values on the current year ('residency').

	Native community				Invasive species	
	Native plant cover		Species richness		*Poa* cover	
	2007	2008	2007	2008	2007	2008
Passenger	12	5	19	11	9	8
Driver	−18	−37	0	0		
Opportunist					−7	−5
Residency	20	13	0	22	62	69

Results

Regarding efficacy of treatments, both soil moisture and nitrogen were elevated in plots corresponding to their respective addition treatments (Tannas 2011). Mean responses to treatments by each of the response variables are provided in Supplementary material Appendix A1 Table A1. Mean responses of *P. pratensis* and native plant biomass are presented in Supplementary Appendix A1 Table A2.

The final SEM fit satisfactorily (Fig. 1c; $\chi^2 = 21.2$, $DF = 16$, $p = 0.171$). For the response variables *Poa*, cover, and richness, we report relevant significant direct and indirect paths in the SEM (see Supplementary material Appendix A1 Table A3 for complete table of significant and insignificant paths, and Supplementary material Appendix A1 Table A4 for means, data ranges, and bivariate correlations). Below we report the variance explained by paths corresponding to the passenger, driver, and opportunist models, and residency effects, as well as total variance explained for each response variable.

Poa

In both years, *Poa* cover was most strongly correlated with the prior years' *Poa* cover. For *Poa* 2007 there was a negative effect due to Cover 2006, a weak positive effect from nitrogen, and a weak positive effect of summer defoliation via Cover 2006. The nitrogen treatment had a weak positive, and Cover 2006 a weak negative, effect on *Poa* 2008, both through *Poa* 2007, and summer defoliation had a weak positive effect through Cover 2006 and then *Poa* 2007.

The total variance explained by the SEM was high in both *Poa* 2007 ($R^2 = 0.78$) and *Poa* 2008 ($R^2 = 0.82$) (Fig. 2c). Residency effects explained the largest amount of variance in *Poa* (62% in 2007; 69% in 2008) (Table 2). Paths corresponding to the passenger model explained 9% of variance in *Poa* 2007 and 8% in *Poa* 2008 (Table 2). Paths consistent with the opportunist model explained 7% of the variance in *Poa* 2007 and 5% in 2008 (Table 2); these net effects were negative.

Cover

The strongest paths to Cover 2007 were from summer defoliation, Cover 2006 (both positive), and *Poa* 2006 (negative) (Table 1). There were weaker indirect effects of summer defoliation (negative) and the nitrogen treatment (positive) on Cover 2007, both via Cover 2006.

The strongest effects on Cover 2008 were from *Poa*, including a strong negative direct correlation with *Poa* 2007, and indirect negative correlation with *Poa* 2006 through *Poa* 2007. Cover 2008 was also positively correlated with Cover 2007. There were some weak, indirect effects on Cover 2008: Cover 2006 through *Poa* 2007, and summer defoliation through Cover 2007 (positive), and *Poa* 2006 through Cover 2007 (negative).

Total variance explained by the SEM for Cover 2007 ($R^2 = 0.50$) and 2008 ($R^2 = 0.55$) were both moderately high (Fig. 2c). Residency effects explained a large amount of variance (20%) in Cover 2007, and 13% of variance in Cover 2008 (Table 2). Paths from the resource/disturbance treatments to cover explained some variance (12% in 2007 and 5% in 2008); however, on closer examination, the net effects of these paths for both years were positive, and thus are not attributable to the passenger model (Table 2). Paths corresponding to the driver model explained a high amount of variance (18%) in Cover 2007, increasing to 37% in 2008.

Richness

The only significant path to Richness 2007 was a positive effect of summer defoliation (Table 1). Richness 2008 was positively correlated with Richness 2007, and weakly indirectly correlated with summer defoliation via Richness 2007 (positive).

The total variance explained by the SEM for richness was relatively low in 2007 and moderate in 2008 (2007 $R^2 = 0.19$; 2008 $R^2 = 0.33$) (Fig. 2c). The driver and opportunist models explained no variance in Richness 2007; all variance explained by the SEM (19%) was due to paths from the resource/disturbance treatments (Table 2). Residency effects explained the highest variance (22%) for Richness 2008, while the paths corresponding to the passenger driver explained 11%, and the driver model explained no variance (Table 2). As with cover, however, the net effects of the paths from the resource/disturbance treatments were positive, and thus are not attributable to the passenger model (Table 2).

Discussion

In both years, we found predominant support for the driver model, and some support for the opportunist model. Consistent with the driver model, *Poa* had a negative effect on the cover component of the native community, the magnitude of which increased from 2007 to 2008; species richness was unaffected. The native community had a negative relationship with *Poa*, consistent with the opportunist model, but these effects were weak compared to those of the driver model. Although the resource and disturbance treatments had a positive effect on *Poa*, the corresponding effects on the native community were positive rather than negative, and thus the effects of the resource/disturbance treatments were not consistent with the passenger model.

By describing all paths over time, we were able to assess temporal variability in mechanism, which is important when determining the processes controlling invasion (Dietz and Edwards 2006). The role of *Poa pratensis* as a driver increased with time as it increased in abundance, largely due to residence effects, but also due to positive effects of the resources/disturbance treatments. This increase in *P. pratensis* due to environmental conditions, and subsequent increased contribution of the driver model, is consistent with the invasion model Bauer (2012) recently coined the ‘back-seat driver’. The ‘back-seat driver’ model is a subset of the driver model, in which underlying environmental conditions aid the invasive species’ initial establishment (such as with the passenger model), but the invasive species assumes the role of driver once established (Bauer 2012).

Our study’s strength is the ability to describe quantitatively multiple, co-occurring paths between the environment, the invasive species, and the native community. The occurrence of multiple, simultaneous models of invasion has been suggested by MacDougall and Turkington (2005) and Didham et al. (2005). Evidence points to the driver model as the dominant explanation for invasion in our system, and the opportunist as a secondary model. As an alternative to testing for only these specific conceptual models, we were also able to describe all relationships contributing to invasion; established models of invasion aided us in interpreting these relationships. Didham et al. (2005) noted that a combination of approaches including structural equation modelling is necessary when assessing the invasion process. Particularly important is the ability of structural equation modelling to assess both indirect and direct relationships and causal, rather than correlative, relationships between variables. For example, without the consideration of indirect relationships, the path from the resource/disturbance treatments to *Poa* (positive) and then to the native community (negative), would appear as a direct, negative relationship between the resource/disturbance treatments and the native community, lending false support to the passenger model.

Of the three invasion models, we found least support for the passenger model in our system; however, a number of studies in both annual (HilleRisLambers et al. 2010) and perennial grassland (MacDougall and Turkington 2005) have shown support for the passenger hypothesis. Differences in study systems, invader biology, or experimental design may explain these findings. For example, MacDougall and Turkington (2005), using *P. pratensis* as well, found predominant support for the passenger, rather than driver, model. This may reflects differences in study context; our study site has a different disturbance regime than that of MacDougall and Turkington (2005), where fire suppression was implicated as a major factor in *P. pratensis* invasion.

Study design can also be important in discerning between passenger and driver models. Our experimental design and analysis framework was capable of identifying the interactions occurring during the invasion process in the field, and attributing them to multiple conceptual models. In the study by HilleRisLambers et al. (2010), the only interactive process measured was competitive ability for nutrients. Our field experiment, however, implicitly included additional interactive processes such as novel weapons involving allelopathy or mycorrhizal networks (Callaway and Ridenour 2004) that could contribute to the success of *P. pratensis* in our system. MacDougall and Turkington (2005) tested community responses to *P. pratensis* removal rather than to the actual process of invasion, which may limit the researcher's ability to determine the original cause of invasion (Didham et al. 2005).

Support for the driver model has been implicated in systems where invasive species have strong competitive ability relative to native species (Vila and Weiner 2004, Bennett et al. 2011). Indeed, a variety of competitive mechanisms have been identified for *P. pratensis:* seedling root competition (Bookman and Mack 1982), light interception (D'Antonio and Vitousek 1992), allelopathy (Lipinska and Wanda 2005), matted growth form (Grilz and Romo 1995) and increased soil nitrogen via litter production (Wedin and Tilman 1990). Support for the driver model has been found in some studies in both annual (Flory and Clay 2010) and perennial (Maron and Marler 2008) grasslands.

As is consistent with the driver model, the invasive species *P. pratensis* negatively affected the native community. However, *P. pratensis* decreased only native plant cover, and not species richness. Indeed, overall variance explained for richness by the SEM was low. Other processes, such as interannual variation in climatic variables, may control richness in this system, or perhaps sustained changes to abundance over time would eventually lead to changes in richness. Flory and Clay (2010) found that native biomass responded quickly to invasion, and only after two years was diversity affected as well.

Consistent with the opportunist model, the effect of the native community on *Poa* was negative. However, this was true for only native cover, not richness. Reduced cover of native species allowed the invasive species to establish, implying support for the resource capture hypothesis: a community with higher productivity implies more complete resource capture by the community and fewer resources available to invaders (MacArthur 1970, Tilman 1982). In this case, promoting a productive native community would be an effective management technique to discourage invasion. As richness did not independently drive invasibility, we find no support for the idea that more diverse communities resist invasion (Tilman 1997). Similarly, Cleland et al. (2004) compared the importance of productivity and diversity in influencing invasion, and found that invasion increased with less productivity, while species richness had no independent effect on invasion.

Of the four disturbance/resource treatments, summer defoliation (except for an initial, transient negative effect) and nitrogen had significant positive effects both on native cover and *P. pratensis* cover, while water and winter defoliation had no significant effects (Table 1). Defoliation is known to have a positive effect on *P. pratensis* (Jung et al. 1974), and the release of plants from accumulated litter which accompanies defoliation may have resulted in increased cover of the native community (Willms et al. 1986). Outside of the growing season, i.e. with winter defoliations, these effects were not evident. Consistent with the observed response to nitrogen, increased resources generally have positive effects on invasive species (Kolb et al. 2002), and native prairie plants (Lamb et al. 2007). However, water had no significant effect on any of the response variables in the SEM; perhaps a more intensive water addition, or a water reduction treatment, would be necessary to elicit significant results, or water acted indirectly through nitrogen via increased nitrogen mobilization (Booth et al. 2005). Environmental effects, however, in the SEM were overall weaker than those of community interactions.

As the driver, back-seat driver and opportunist model all contributed to *P. pratensis* invasion, following corresponding management actions will aid in preventing invasion. In the case of the back-seat driver model, factors corresponding to the environment's positive effect on *P. pratensis*, mainly summer defoliation and elevated nitrogen, should be limited. Corresponding to the opportunist model, maintenance of a productive native community will aid to prevent invasion. However, the strong residency effect of *P. pratensis* and increase in strength of driver model over time suggest that without direct reduction in *P. pratensis*, control of this invasive species is likely to be unsuccessful. Our results suggest that management techniques that directly reduce *P. pratensis* abundance, such as manual removal, herbicide control, and biological control, rather than reduction in grazing intensity, will be most effective.

Conclusion

We quantitatively described the relationships between factors thought to be involved in the process of *P. pratensis* invasion, and determined how they agree with established conceptual models of invasion. We found evidence to support both the driver and opportunist models in this system. Understanding the invasion process is essential to determining appropriate management action and invasive species management should be guided by studies that are capable of integrating the complexity of interactions between the invasive species, the native community, and the environment simultaneously. We concluded that management activities that directly reduce *P. pratensis* abundance should be most effective.

Acknowledgements – We thank Andrew S. MacDougall and Olivier Chabrerie for their discussions on data interpretation, and C. Guillermo Bueno for his editing. Funding was provided through a National Sciences and Engineering Research Council (NSERC) Discovery Grant and Accelerator Support to JFC. Funding for field work was provided to SCT and EWB through Alberta Sustainable Resource Development (SRD), Alberta Conservation Association (ACA), Apache Canada Ltd., and Compton Petroleum Corporation.

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Supplementary material (available as Appendix O20951 at < www.oikosoffice.lu.se/appendix >). Appendix A1.