ORIGINAl RESEARCH

Long-term sand dune spatio-temporal dynamics and endemic plant habitat extent in the Athabasca sand dunes of northern Saskatchewan

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Abstract
The Athabasca sand dunes in northern Saskatchewan and north-east Alberta are a unique landscape of moving sand that hosts nine narrowly distributed endemic vascular plant taxa. We modeled the extent of habitat for each species, corresponding dune morphologies in species habitat, spatial and temporal variation in dune environments, and rates of woody vegetation encroachment at dune boundaries to support an assessment of long-term threats for the Athabasca endemic dune flora. Landsat images were used to maximize the time spans and areal coverage of the study. The Athabasca sand dunes are currently active and characterized morphologically by crescentic ridge and morphodynamically by transverse form dunes. Longitudinal sand movement parallel to the dune axis resulted in the creation of new dune areas along the east and south-east boundaries of the dune fields at a rate of 0.14 km² year⁻¹. Forest succession along the western boundaries of the dune fields resulted at an annual dune loss of 1.98 km² year⁻¹. The net extent of dune stabilization between 1985 and 2014 was 53.76 km² or nearly 20 percent of the total open sand dune extent. All habitat modeling methods showed robust performance (>0.5 AUC), with the best performance in most cases from generalized linear models. Estimated total available/occupied habitat was comparatively low for the least abundant species Achillea millefolium (38.92 km²) and Armeria maritima (48.82 km²), and of those areas 53.5% and 16.29%, respectively, are influenced by dune stabilization. Continuing stabilization of the Athabasca sand dunes region may present conservation concerns for these narrowly distributed endemic taxa.

Introduction
The Athabasca sand dunes in northern Saskatchewan and north-east Alberta are the largest complex (~349 km²) of active sand dunes in Canada and are one of the most northerly active sand dune formations on earth. This unique boreal landscape is characterized by large areas of active sand dunes and a unique cluster of nine narrowly distributed endemic plant species adapted to an environment of moving sand (Raup 1936; Argus and Steele 1979;
Raup and Argus 1982; Macdonald et al. 1987; Cooper and Cass 2003; Lamb and Guedo 2012). These species are *Achillea millefolium* var. *megacephala* and *Tanacetum huronense* var. *floccosum* (both Asteraceae), *Armeria maritima* ssp. *interior* (Plumbaginaceae), Deschampsia mackenzieana (Poaceae), *Salix brachycarpa* var. *psamnophila*, *Salix silicicola*, *Salix turnorii*, *Salix tyrrellii* (Salicaceae) and *Stellaria arenicola* (Caryophyllaceae). With the exceptions of *Salix tyrrellii* and *Stellaria arenicola* (‘Not at Risk’), the Athabasca sand dunes endemic flora are currently listed as ‘Species of Special Concern’ under the Canadian Species at Risk Act (SARA). These taxa were first described by Raup (1936), and while not all are currently recognized by Flora of North America Editorial Committee (1993), these taxa are clearly morphologically and genetically distinct from locally co-occurring congers (e.g. Purdy and Bayer (1996) and Purdy and Bayer (1995)). Additionally, as the taxa are listed under SARA, updated status assessments are required regardless of taxonomic status. As sand dune systems are highly dynamic in nature, the extent, distribution pattern and changes to the preferred habitat is a major knowledge gap for a comprehensive reassessment of the status of these species. We used remote sensing techniques to investigate morphologies and expansion process of sand dunes, long-term trends of vegetation establishment and endemic plant habitat trends in the Athabasca sand dunes.

Species of conservation concern typically have relatively small populations. The sampling of such species result small sample sizes influencing on the statistical power and model robustness (Stockwell and Peterson 2002; Thuiller et al. 2004; Guisan et al. 2006; Pearson et al. 2007; Wisz et al. 2008). Relatively few studies have evaluated the effectiveness of different modeling algorithms with limited occurrence data for species specialized in dune environments (Wisz et al. 2008; Williams et al. 2009; Gogol-Prokurat 2011). We compared five different species distribution modeling algorithms generalized linear models (GLM), generalized additive models (GAM), multivariate adaptive regression splines (MARS), classification and regression trees (CART) and artificial neural networks (ANN) with remotely sensed predictors to model the distribution of the Athabasca endemic plant species. Comprehensive field assessments of sand dune environments are limited by logistical considerations, particularly in remote sites such as the Athabasca sand dunes (Carson and MacLean 1986; Paisley et al. 1991; Wolfe et al. 2001; Okin and Painter 2004; Wood et al. 2012). The use of remotely sensed data and global information systems (GIS) are an important part of sand dune environment analysis, as it enables studies across both greater spatial scales and more extended periods of time (Hugenholtz 2005a,b; Ewing and Kocurek 2010; Mohamed and Verstraeten 2012). The effectiveness of these remote sensing tools and approaches are well characterized, and use has been encouraged by low cost availability of remotely sensed data (U.S. Geological Survey, 2014).

Extensive research has been conducted on the Athabasca endemic flora exploring species morphological differences, taxonomic relationships, environmental/habitat affinities, ecological relationships, distribution patterns and potential threats (Raup 1936; Argus and Steele 1979; Raup and Argus 1982; Macdonald et al. 1987; Cooper and Cass 2003; Lamb and Guedo 2012; Guy et al. 2013). The Athabasca sand dune endemic vascular plant species are highly adapted to an environment of moving sand, and are rarely found in the forested landscapes around the dune fields (Raup and Argus 1982; Macdonald et al. 1987; Cooper and Cass 2003; Lamb and Guedo 2012). Evaluating regional-scale changes to the extent of the open sand environment and resulting changes in species distributions are critical to a long-term threats assessment of the Athabasca endemic flora. Our objectives are threefold: (1) to assess the population size and habitat extent for each endemic species, (2) better understand the dune environment by evaluating dune morphologies, long-term dune spatio-temporal variations and (3) assess rates of woody vegetation encroachment and dune stabilization to evaluate an important potential threat to the Athabasca endemic flora.

**Materials and Methods**

**Study area**

The Athabasca sand dunes in northern Saskatchewan and Alberta is the largest complex of active sand dunes in Canada (58°42′ N; 108°42′ W) with a total extent of ~349 km² (Raup and Argus 1982; Carson and MacLean 1986). The largest dune field comprises two major areas on the west (William River dune field) and east (Thompson Bay dune field) sides of the William River valley. A third main dune field (McFarlane River dune field) is on the west side of McFarlane River valley. A number of smaller dune fields are interspersed in between the major fields (Fig. 1). Annual rainfall and the total precipitation including snow in the region are on average ~250 mm and ~370 mm respectively (Government of Canada, 2015). The climate is comparatively dry in the early part of the summer (May–June) and the beginning of fall (August–October). Total monthly rainfall ranges from ~20 to 70 mm during summer months (Government of Canada, 2015). The highest average temperature of the region reaches ~18–20°C in mid-summer (Government of Canada, 2015).
Field data collection

Ground-truthed data for species and habitat used for this study come from an extensive field survey conducted in 2009 and 2010 to assess populations distribution patterns, and the ecological relationships of the Athabasca endemics (Lamb et al. 2011; Lamb and Guedo 2012). We surveyed 224 randomly pre-located 250 m transects running east to west on a constant northing (Lamb et al. 2011; Lamb and Guedo 2012). A detailed map of the transects and description of the allocation process available in Figure S1. All endemic species individual presence/absences of the target taxa were surveyed in a 10-m-wide transect for willow species and a 4-m-wide transect for grasses and forbs.

Satellite imagery and pre-processing

Two Landsat 5 TM images acquired on September 23rd, 2009 and July 8th, 2010 the closest possible date matches to field survey were used to develop species distribution maps (Referred hereafter as the 2009 and 2010 images). The 30 m spatial resolution of the Landsat images was not adequate to analyze sand dune dynamics on a seasonal or annual basis. Therefore, three image pairs covering the longest possible timespan were selected to assess long-term trends in dune field extent. Images for multi-temporal environment change analysis were selected to have close Julian dates to minimize seasonal variation in vegetation phenology and reflectance characteristics (Jensen 2005). The selected images were acquired on July 3rd,
Overview of methods and objectives

Habitat occupancy modeling for endemic species was performed using five different modeling algorithms categorized under modern regression and machine learning techniques. Only the 2009 and 2010 images were used for this purpose and the likelihood of habitat occupancy of all nine endemic species were separately modeled using the most precise modeling technique selected from the training process. The Bi-Temporal Layer Stack (BTLS) technique was used to illustrate sand dune morphological features and spatio-temporal changes using the 1985 and 2014 image pair. The Post-classification Comparison Change Detection (PCCD) procedure was used to understand how sand dune encroachment occurs into surrounding vegetation and how vegetation encroachment occurs into sand dune fields. Rates of land cover change between sand and vegetation were estimated using 1985 as a base year for the 2002, 2007 and 2014 images separately. The direction and movement distance of sand dunes and surrounding vegetation at dune field boundaries was estimated using generalized additive models (GAM). Finally, long-term temperature, wind and precipitation data from regional weather stations were examined to identify the climate influences on large-scale sand dune field changes. A graphical summary of the overall process is available in Figure S2, and details of all steps followed for each method are available in File S2 – Detailed Methods.

Athabasca endemic plant habitat modeling

The modeling began with observations of species presence/absence, and identification of associated predictor variables likely to influence or describe the habitat and/or species occupancy. The training process links predictors with species presence/absence in geographical space to estimate the likelihood that the species is present or absent in un-sampled locations. Modeling techniques used in the study were from two groups: modern regression and machine learning algorithms as no studies have focused on modeling sparsely distributed species in dune habitats (Elith and Graham 2009; Elith and Leathwick 2009; Franklin and Miller 2009). Modern regression techniques tested include generalized linear models (GLM), generalized additive models (GAM) and multivariate adaptive regression splines (MARS). Machine learning algorithms tested include classification and regression trees (CART) and artificial neural networks (ANN).

We used measures that are independent of the event in the sample, commonly called as threshold-independent measures of accuracy to select the most suitable method for modeling target plant species occurrences (Franklin and Miller 2009). These include the ‘area under the curve’ (AUC) of the receiver-operating characteristic (ROC) plot. ROC is a graph of the false positive error rate on the x-axis versus the true positive rate on the y-axis corresponding to each possible value of threshold probability; AUC is calculated by summing the area under the ROC curve where the value is >0.5 (performance better than random). AUC is a reliable measure for model comparisons as AUC is not affected by changes in species prevalence (Manel et al. 2001; Franklin and Miller 2009). The most precise modeling algorithm for each target species was selected from an iterative process with 1000 iterations for each species and algorithm combination. Average AUC of the 1000 iterations was calculated; the method with the highest average AUC was selected for final species occupancy modeling. Welch’s One-way Analysis of Variances procedure and Games-Howell pair-wise mean comparison was used to illustrate differences and/or similarities of mean AUC among modeling algorithms for a given species (Sheskin 2003). Both Welch’s ANOVA and the Games-Howell method are known to be robust where variances among factors are unequal (Sheskin 2003).

Predictive maps of each species were developed in ArcGIS Model Builder using the best model for the 2009 and 2010 analysis, and the location predictions were averaged for each species final prediction probability maps. Prediction accuracies were evaluated using 30% of ground truth data held back from the model training process. A series of threshold probabilities (0.5, 0.6, 0.7, 0.8, 0.9, 0.95 and 0.99) were used to illustrate changes in error of commission, error of omission, overall accuracy and kappa statistic. Sand dune stabilization influences on available habitat area estimates were also assessed based on the above thresholds to identify the most appropriate thresholds in this context.
Analysis of sand dune morpho-dynamic characteristics

Analysis of sand dune morphological features and migration patterns were used to examine dune activity between 1985 and 2014. When the same spectral band from either three or two different dates is mounted to red, green and blue color guns (Write Function Memory banks), the change in reflectance is displayed in a different color (Bi-Temporal Layer Stack; BTLS) (Mohamed and Verstraeten 2012). In instances where dune mineralogy is homogeneous, <35% vegetation cover and no biogenic-soil crust, changes in sand dune reflectance profiles are controlled mainly by illumination and shading effects from the orientation of the dune crest toward sun azimuth and elevation angles (Paisley et al. 1991; Levin et al. 2004; Okin and Painter 2004). Single dune and dune field scale analyses have shown that the most important feature for the study of sand dune morphological variation is the dune crest, as the crest always has high reflectance relative to other dune features in Landsat – NIR band width (0.76–0.90 μm) (Paisley et al. 1991; Levin et al. 2004; Tsoar 2004; Ewing et al. 2006; Livingstone et al. 2007; Mohamed and Verstraeten 2012). Therefore, this study used dune crest and/or slip-face migration as a spectrally stable feature to identify sand dune morphological features and spatio-temporal variation.

Analysis of sand dune creation and vegetation encroachment

Post-classification Comparison Change Detection (PCCD) was used to measure both sand dune encroachment into

![Graph showing mean AUC of ROC plot for 2009 and 2010](image)

**Figure 2.** Modeling algorithm performance evaluation based on the area under the curve (AUC) of receiver-operating characteristic plot (ROC). The Y-axis is the mean AUC of the ROC value for each species and each modeling algorithm. Each bar for a species represents the calculated mean AUC of one thousand iterations of a particular algorithm. Species abbreviations refer to Tanacetum huronense var. floccosum (TANHUR), Stellaria arenicola (STEARE), Salix tyrellii (SALTYR), Salix turnorii (SALTUR), Salix silicicola (SALSIL), Salix brachycarpa var. psammophila (SALBRA), Deschampsia mackenzieana (DESMAC), Armeria maritima ssp. Interior (ARMMAR), and Achillea millefolium var. megacephala (ACHMIL). Modeling techniques include generalized linear models (GLM), generalized additive models (GAM), multivariate adaptive regression splines (MARS), random forest (RF) and artificial neural networks (ANN).
surrounding forest vegetation and vegetation encroachment into stabilized sand dune fields. Comparisons were made using the 1985 image as the base year to the 2002, 2007 and, 2014 images. An unsupervised classification approach was selected as a-priori detailed regional landcover classes were not available. Twenty spectral classes were initially requested using the Iterative Self-Organizing Data (ISODATA) algorithm. Similar classes were merged to obtain three distinct land cover classes: water, vegetation and open sand. Next, the classified 1985 base year image was compared with a classified 2014 image on a pixel-by-pixel basis using a change detection matrix (Jensen 2005; Neigh et al. 2008). A from-to analysis was carried out to identify land cover changes from vegetation to sand and from sand to vegetation using Engineering Analysis and Scientific Interface (EASI) modeling in PCI Geomatica 2016 – Focus (Jensen 2005; Neigh et al. 2008).

The two techniques; BTLS and PCCD, however, were not able to clearly prove the sectors of the dune field boundaries where dune creation and vegetation encroachment had occurred. We therefore, evaluated changes in reflectance values along the dune edges using 1985 as the base year to the years 2002, 2007 and, 2014. A series of 500 m long sampling transects crossing the dune edge were created every 1 km along the boundaries (Fig. S3 and S4) and the reflectance values of each pixel underneath each transect were extracted to evaluate reflectance variations over time. Since sand has higher reflectance than vegetation, a positive reflectance difference indicates dune migration into surrounding vegetation and negative differences indicates vegetation encroachment into sand dune fields.

Reflectance differences for each image pair (2002, 2007 and, 2014) to 1985 were modeled as a function of distance along the transects using Generalized Additive Models (GAM). GAM is a nonparametric extension of the Generalized Liner Model (GLM) and a convenient method to model nonlinear relationships when there is no prior expected shape to the curve (Hastie and Tibshirani 1990; Wood 2006). All statistical analyses were implemented in the R 3.1.2 software environment and the GAM was done using the ‘gam’ function in the mgcv library (Wood 2006; R Core Team 2014). Directional categories were separately analyzed to identify predominant directions of sand dune expansion into vegetation and vegetation encroachment into sand dunes.

**Table 1. Mean area under the curve (AUC) comparison among different modeling algorithms for each plant species. The abbreviations are explained in Figure 2.**

| Plant Species and Year of Field Survey | Welch’s Test -P value | Games-Howell pairwise mean AUC comparisons and grouping |
|----------------------------------------|-----------------------|-------------------------------------------------------|
|                                        | GLM                   | GAM                     | MARS                  | RF                    | ANN                  |
| 2009 TANHUR                            | -0.00001              | 0.70404^A               | 0.67428^C             | 0.68464^B             | 0.70071^A           | 0.68004^B           |
| STEARE                                 | -0.00001              | 0.76347^A               | 0.78852^D             | 0.75228^B             | 0.72050^D           | 0.74099^D           |
| SALTYR                                 | -0.00001              | 0.88121^A               | 0.76492^D             | 0.84582^B             | 0.83111^C           | 0.84135^C           |
| SALTUR                                 | -0.00001              | 0.83044^A               | 0.76468^D             | 0.81707^B             | 0.76509^D           | 0.78389^C           |
| SALSIL                                 | -0.00001              | 0.80436^A               | 0.78830^B             | 0.78859^B             | 0.74952^C           | 0.79146^B           |
| SALBRA                                 | -0.00001              | 0.84731^A               | 0.73274^D             | 0.83385^B             | 0.80933^C           | 0.81177^C           |
| DESMAC                                 | -0.00001              | 0.71878^A               | 0.72370^A             | 0.71313^B             | 0.69717^D           | 0.69501^D           |
| ARMMAR                                 | -0.00001              | 0.74262^A               | 0.69189^B             | 0.69055^D             | 0.67615^C           | 0.67615^A           |
| ACHMIL                                 | -0.00001              | 0.87346^A               | 0.66640^E             | 0.82711^D             | 0.85904^B           | 0.84459^C           |
| 2010 TANHUR                            | -0.00001              | 0.65215^B               | 0.63649^C             | 0.64785^B             | 0.70591^A           | 0.64992^A           |
| STEARE                                 | -0.00001              | 0.59273^C               | 0.66997^B             | 0.64304^C             | 0.69059^A           | 0.60836^D           |
| SALTYR                                 | -0.00001              | 0.72060^A               | 0.69598^C             | 0.71238^B             | 0.71069^B           | 0.71248^B           |
| SALTUR                                 | -0.00001              | 0.69428^B               | 0.69289^B             | 0.68453^C             | 0.71500^A           | 0.65775^D           |
| SALSIL                                 | -0.00001              | 0.71709^A               | 0.68501^B             | 0.69441^B             | 0.67657^D           | 0.69348^B           |
| SALBRA                                 | -0.00001              | 0.73145^A               | 0.71409^C             | 0.72411^B             | 0.70143^D           | 0.71250^C           |
| DESMAC                                 | -0.00001              | 0.752754^A              | 0.749688^A            | 0.739501^B            | 0.712835^C          | 0.742380^B          |
| ARMMAR                                 | -0.00001              | 0.68492^A               | 0.61021^C             | 0.58701^C             | 0.55524^D           | 0.62506^B           |
| ACHMIL                                 | -0.00001              | 0.76801^A               | 0.64313^C             | 0.74405^B             | 0.74057^B           | 0.64192^C           |

The Analysis of Variance (ANOVA) procedure for mean comparison purpose tested null hypothesis of all means are equal, against alternative hypothesis of at least one mean is different at significance level 0.05. The Welch’s test was used in this analysis as equal variances were not assumed among treatment levels. The mean comparison was assessed using Games-Howell Pairwise Mean Comparisons. Means that do not share a letter are significantly different among modeling techniques along each species and highest reported AUCs are in bold.

Analysis of Climatic Factors

In general, sand dune environments are influenced by long-term wind and rainfall patterns (Carson and MacLean...
1986; Wolfe et al. 2001; Tsoar 2004, 2005; Hugenholtz 2005a,b; Hugenholtz et al. 2012; Wood et al. 2012; Al-Masrahy and Mountney 2013). Long-term climatic data for the study were obtained from the Environment Canada – Fort Chipewyan (58°46” N; 111°07”W) weather station located approximately 115 km south-east of Athabasca dune fields, as this was the closest station with long-term weather data available (Carson and MacLean 1986). Monthly directional wind patterns were examined by summarizing hourly wind direction readings separately by month from 1971 to 2015. Rain fall, snow fall, total precipitation and temperature data were examined from 1967 to 2006 (changed timespan based on data availability). Mean monthly total rain fall, mean monthly total snowfall, mean monthly total precipitation, mean monthly temperature, total annual rainfall and, total annual precipitation were analyzed to understand how seasonal variation may influence wind action on exposed sand.

**Results**

**Athabasca endemic plant habitat modeling**

The mean AUC for all species, analytical algorithm and year combinations were above 0.5 (Fig. 2), indicating that all model algorithm performances were better than random and capable of successfully modeling each species. Welch’s One-way Analysis of Variance procedure confirmed ($P < 0.05$) significant differences in performance among algorithms (Table 1). The 2009 Games-Howell

![Figure 3. Predicted likelihood of suitable habitat distributions for Athabasca endemic plant species. Probability of suitable habitat within a pixel for each of the Athabasca endemic species. The color ramp uses ten categories with 0.1 increments. Warm colors indicate higher probability and the cooler colors lower probability of finding suitable habitat.](image-url)
pair-wise mean comparison showed that GLM mean AUC was significantly higher for all species with the exception of Deschampsia mackenzieana (GAM highest AUC but GLM and GAM mean AUC’s not significantly different). The 2010 data had GLM performance as the highest except for Deschampsia mackenzieana, Stellaria arenicola and Salix turnorii (RF classification algorithm). The best algorithm for each species and year combination was used to develop a prediction map (Fig. 3).

We estimated the influence of sand dune stabilization on the extent predictions for each species over a range of threshold probabilities to demonstrate the assessment uncertainty associated with predictions at each level of threshold. Errors of commission, omission, overall accuracy and kappa statistic were evaluated and the result shows optimum levels are between 0.5 and 0.7 threshold probability range for species in consideration (Fig. S5). Estimated total of available/occupied habitat and the extent of the stabilized/affected proportion of the habitat gradually decreased with increases in threshold. Slope variation of estimated total occupied habitat extent in relation to increase in threshold were consistent (Lower extent estimates for least abundant species and vice versa) below 0.6 threshold and the prediction patterns are largely random above that point (Fig. 4 and Table S2). For example the estimated extent of the rare Achillea millefolium and widespread Deschampsia mackenzieana were 38.92 km² and 89.52 km², respectively, at a 0.6 threshold, in comparison to 17.12 km² and 9.52 km² at the 0.8 threshold. More details of total occupied habitat extent estimate (km²), stabilized habitat extent between 1985 and 2014 (km²) and percent of most probable habitat influenced by sand dune stabilization based on varying thresholds is available in Table S2.

Sand dune morpho-dynamic characteristics

The BTLS analysis revealed that the crests of the sand dunes were generally aligned in a north-west and south-east direction with dune structures were approximately straight or gently curved along the main axis (Fig. 5A). The Athabasca sand dune region is comparatively dry (Fig. 6) throughout the summer (May to July) and the beginning of fall (August–October) suggesting that winds during this period may dominate dune field migration patterns. The late-summer – early fall period is dominated by winds from the south-east and east (Fig. 7). However, winds throughout the summer and early fall from the north-west to south-west range may influence longitudinal sand movement along the dune axis (Fig. 7). The BTLS results and wind data demonstrate that the dune migration direction is almost parallel and the main
axis of the dunes perpendicular to the prevailing wind pattern. The majority of dunes can thus be classified as ‘crescentic ridge’ in external morphological terms and ‘transverse’ in morpho-dynamic terms. Complex red-cyan patterns observed at the ends of individual sand dunes and several large areas in the William River and Thompson Bay dune fields indicate less distinct spectral profiles (Fig. 5B) arising from gently undulating to flat sand surfaces.

Sand dune creation and vegetation encroachment

The PCCD results indicate that changes from vegetation to sand (red) during the period of 1985 to 2014 were most prominent on the east and south-east margins of each sand dune field (Fig. 8A and B), with the exception of the east edge of William River dune field where it borders the river. Overall, this indicates that sand dune creation occurs mainly at the east and south-east edges of each dune field. The estimated area of sandy surfaces created between 1985 and 2014 was 4.20 km² and the rate of change was 0.14 km² per year (Table 2). In contrast, green, indicating land cover changes from sand to vegetation during the period of 1985 to 2014, is more prominent on the west edge indicating a general pattern of forest encroachment on that edge (Fig. 8A and B). The estimated area of sandy surface occupied by woody vegetation was 57.55 km² and the rate of change was 1.98 km² per year (Table 2). The rate of vegetation encroachment into the sand dunes is thus approximately 9 times higher than new sand dune creation resulting in a net loss of dune area from 1985 to 2014 of 53.76 km². Annual rates are variable as the estimated average annual rate of dune area lost from 1985 to 2002 was 1.15 km² per year, but 1985 to 2014 estimates were an average of 1.85 km² lost per year (Table 3).

GAM by directional category was used to estimate the distance and directional movement of sand dunes and vegetation at the dune boundaries. Overall, results were in line with the PCCD analysis with significant positive reflectance differences the south-east and east directions across all three comparisons from 1985 to 2002, 2007 and, 2014 (Table 4). This indicates that creation of sand dunes occurs most commonly on the east and south-east dune margins at a rate of 3.28 m year⁻¹ (Table 5, panel d and h of Figure S6, Figure S7 and, Figure S8). Negative reflectance differences indicating vegetation encroachment were significant on the western dune boundaries indicating encroachment at a rate of 5.85 m year⁻¹ across all three comparisons (Table 4, Table 5, panel a of Figure S6, Figure S7 and, Figure S8).

Discussion

Analysis of species occurrence likelihood of Athabasca endemics

We modeled endemic species habitat distributions to identifying the likelihood of habitat occupancy of nine endemic vascular plant species observed in Athabasca sand dunes. The effectiveness of five algorithms were
evaluated in light of the sparse distribution of the species and low spatial resolution of predictors. All methods showed robust performance (>0.5 AUC), however, strong GLM performance likely arises from strong linear relationships between species habitat occupancy and Landsat 7 reflectance bands. The literature highlights that habitat specialists are often more accurately modeled than generalists because of their reliance on spatially restricted and spectrally distinct environmental conditions (Guisan et al. 2006; Franklin and Miller 2009). However, we were constrained in this analysis by the 30 m spatial resolution and strongly believe that the observed uncertainties may have been avoided with high resolution imagery. This applies most strongly for Armeria maritima and Achillea millefolium as they are the least abundant of the species and are restricted, respectively, to limited habitats in gravel pavements and wet inter-dune slacks scattered among the active dunes (Lamb and Guedo 2012).

Analysis of available/occupied habitat extent in relation to varying probability thresholds is a good illustration of how habitat predictions can be influenced by threshold probabilities. All species had a decreasing trend of

Figure 6. Rainfall, snowfall, total precipitation and temperature. Daily readings of total rainfall and average temperature from the Environment Canada – Fort Chipewyan (58°46' N; 111°07' W) weather station located approximately 115 km south-east of Athabasca dune fields. The data were averaged across 1967 to 2006 to obtain monthly values. (A) Average monthly total rainfall, snowfall and, total precipitation. (B) Average monthly temperature. (C) Total annual rainfall and total precipitation.
estimated occupied habitat with increasing threshold probability. The rare habitat specialist species *Achillea millefolium* and *Armeria maritima* had very low estimated occupied proportion relative to common species such as *Deschampsia mackenzieana* that had a large observed habitat extent. Similar trend of estimated relative abundances were observed between the 0.5 and 0.6 threshold levels, however, the pattern of relative abundances drastically deviates from observed pattern beyond the threshold 0.6. On the basis of this, we used a 0.6 threshold as our cut-off probability to illustrate sand dune stabilization influences on habitat for each species.

*Achillea millefolium* habitat was the most influenced by sand dune stabilization with an estimated total available/occupied habitat of 38.92 km² (11.14% of total dune area) and 53.5% of that area potentially influenced by stabilization. *Armeria maritima* had 48.82 km² (13.97% of dune area) of available/occupied habitat and but only 16.29% potentially influenced by dune stabilization. The habitat generalist *Deschampsia mackenzieana* in contrast occupies 89.52 km² (25.63% of the dune area) with only 9.18% of that area influenced by stabilization. *Salix brachycarpa*, *Salix silicicola*, *Salix turnorii*, *Salix tyrrellii*, *Stellaria arenicola* and *Tanacetum huronense*, respectively, had 37.78, 37.22, 34.21, 35.58, 44.20 and 37.55 percent of occupied habitat potentially affected by stabilization.

The risk of stabilization may be of an importance to the long-term viability of the populations of the less abundant endemic species, particularly *Achillea millefolium* (Lamb et al. 2011; Lamb and Guedo 2012). *Armeria maritima* is found in very low numbers only on gravel pavements and occasionally in wet inter-dune slacks; the species is absent from active dunes as it cannot tolerate burial (Lamb and Guedo 2012). Gravel pavements are generally found near the center of the dune fields, however, and are thus at low risk of stabilization. *Achillea millefolium* is potentially more vulnerable to stabilization. It was the second least abundant

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**Figure 7.** Monthly directional variations in wind pattern. Summary of hourly readings of wind direction obtained from Environment Canada – Fort Chipewyan (58°46’N; 111°07’W) weather station located approximately 115 km south-east of Athabasca dune fields. The true direction from which the wind is blowing measured in 10s of degrees. The wind rose plot summarizes the direction by 20-degree increments and each paddle represents proportion of wind observations from that angle. Measurements were recorded through 360 degrees and a calm wind is recorded as 0 degrees. The frequency variations of wind direction were analyzed on a monthly basis from 1971 to 2015. Only wind direction data (no speed data) were available for the time period reported.
species observed during the field survey and is frequently found in wet inter-dune slacks and secondarily on lichen crowberry heaths and woodlands near dune edges (Lamb and Guedo 2012). The presence of Achillea habitat near the dune margins likely drives the very high percentage of habitat potentially affected by stabilization, and suggests that conservation concern for this species may be warranted.

Wide habitat preferences ensure the availability of abundant suitable habitat for the more common endemic species (Deschampsia mackenzieana, Salix brachycarpa, Salix silicicola, Salix turnorii, Salix tyrrellii, Stellaria arenicola and Tanacetum huronense). That, combined with the relatively large populations (Lamb and Guedo 2012), suggests low conservation concern for those species. The extent of the wet inter-dune slacks remains an important question, however, as that habitat is a site of high recruitment for Salix brachycarpa, Salix silicicola, Salix turnorii, Salix tyrrellii, Achillea millefolium and Tanacetum huronense (Lamb and Guedo 2012). A long-term understanding the distribution of this habitat is important as it supports higher endemic species richness and total abundance than anywhere else on the landscape.

**Sand dune morpho-dynamic characteristics**

We observed many transverse-crescentic ridges in the McFarlane river area (Fig. 5A) migrating in a northeasterly direction. The crescentic ridge classification is based on the external morphology of depositional forms (shape) of the dunes, and is typically straight or very gently curved at both ends. The formation of crescentic dunes starts from individual crescents that coalesce laterally when deposition of sand increases. Transverse dunes imply a morpho-dynamic process driven by wind with sand movement and dune migration toward the prominent wind direction and the main dune axes perpendicular to the wind direction (McKee 1979; Lancaster 1995; Mohamed and Verstraeten 2012). Carson and MacLean (1986), made similar findings in the Athabasca dunes system, noting the abundance of transverse sand dunes migrating toward the north-east. Furthermore, they identified longitudinal processes that were likely driving sand dune lateral coalition and elongation. Although crescentic ridge features are very clearly visible at the center of single dunes in the BTLS maps, the features are compound at both ends reflecting lateral coalition processes were active in the past. Frequent winds from the west-northwest and east-south-east in July–October (Fig. 7) may contribute significantly to lateral coalition and elongation processes.

Compound dune morphologies are common in the William River and Thompson Bay dune fields (Fig. 5B). The very complex red and cyan pixel patterns make the distinction of simple morphological variation using the BTLS procedure difficult. However, positional changes in high reflectance areas are an indication of dune crest changes over time. The field work of Carson and MacLean (1986), confirms that the area was composed of transverse-crescentic ridges and gently undulating to flat sand surfaces. This
can result in similar reflectance profiles throughout the area which are difficult to distinguish at the 30 m spatial resolution of Landsat images. According to Lancaster (1995), compound crescentic ridges are characterized by superimposed multiple crescentic ridges on the upper stoss and crestal areas of the major crescentic ridge. This is most likely the reason for the complex red-cyan pixel patterns as crescentic ridges are formed by individual crescents coalescing laterally when deposition of sand increases. Furthermore, analysis of compound crescentic ridge dune

Table 2. Post-Classification Comparison Change Detection (PCCD) estimate of total sand dune creation and dune stabilization from 1985 to 2002, 2007 and 2014.

| Duration | Number of years | Number of pixels | Extent of vegetation encroachment (km²) | Rate of vegetation encroachment (km² year⁻¹) | Number of Pixels | Extent of sand dune creation (km²) | Rate of sand dune creation (km² year⁻¹) |
|----------|-----------------|------------------|----------------------------------------|---------------------------------------------|-----------------|-----------------------------------|---------------------------------------|
| 1985–2002 | 17              | 26280            | 23.65                                  | 1.39                                        | 4145            | 3.73                              | 0.22                                  |
| 1985–2007 | 22              | 31963            | 28.77                                  | 1.31                                        | 3681            | 3.31                              | 0.15                                  |
| 1985–2014 | 29              | 63945            | 57.55                                  | 1.98                                        | 4670            | 4.20                              | 0.14                                  |
| Marginal means | 36.66          | 1.56             |                                         |                                             | 3.75            | 0.17                              |                                        |

The table illustrates total sand dune creation and stabilization estimates of Post-Classification Change Detection process. Number of pixels was converted to square kilometers using 30 m spatial resolution of Landsat images used. The net creation or reduction of the dune area for each year was an estimate in comparison to 1985 base year. The rate of reduction was calculated considering the time gap between 1985 and the recent year in consideration.

Table 3. Total sand dune net loss and the rate of change estimate from 1985 to 2002, 2007 and 2014.

| Year | Number of Pixels | km² | Reduction of the dune area (km²) | Number of years | Rate of reduction (km² year⁻¹) |
|------|------------------|-----|---------------------------------|-----------------|-------------------------------|
| 1985 | 293 327          | 263.99 | NA                              | NA              | NA                            |
| 2002 | 271 667          | 244.50 | 19.49                           | 17              | 1.15                          |
| 2007 | 265 027          | 238.52 | 25.47                           | 22              | 1.16                          |
| 2014 | 233 595          | 210.24 | 53.76                           | 29              | 1.85                          |

The table illustrates total open sand dune area of each year classified using unsupervised classification technique. Number of pixels was converted to square kilometers using 30 m spatial resolution of Landsat images used. The net reduction of the total dune area for each year was an estimate in comparison to 1985 base year. The rate of reduction was calculated considering the time gap between 1985 and the recent year in consideration.

Table 4. Generalized Additive Modeling (GAM) results of directional movement and distance analysis of sand dune creation and vegetation encroachment in the study area.

| E-W   | N-S  | NE-SW | NW-SE  | S-N   | SE-NW | SW-NE  | W-E  |
|-------|------|-------|--------|-------|-------|--------|------|
| 1985–2002 | A   | 4.564 | 1.001  | 1.001 | 3.903 | 1.001  | 2.162 | 1.000 | 5.148 |
|        | B   | 16.534| 8.559  | 8.113 | 9.144 | 9.332  | 8.451 | 10.420| 18.040|
|        | C   | <0.001| 0.003  | 0.004 | <0.001| 0.002  | <0.001| 0.001 | <0.001|
| 1985–2007 | A  | 6.120 | 2.257  | 1.002 | 7.483 | 1.002  | 1.524 | 1.001 | 7.326 |
|        | B  | 15.210| 2.778  | 2.407 | 9.202 | 0.782  | 1.417 | 1.265 | 13.597|
|        | C  | <0.001| 0.043  | 0.120 | <0.001| 0.007  | 0.377 | 0.238 | 0.260 |
| 1985–2014 | A  | 6.443 | 5.604  | 1.003 | 7.492 | 1.001  | 2.068 | 1.000 | 7.596 |
|        | B  | 19.031| 4.670  | 0.000 | 10.367| 1.542  | 2.130 | 31.246| 21.030|
|        | C  | <0.001| 0.001  | 0.997 | <0.001| 0.014  | 0.103 | <0.001| <0.001|

Generalized Additive Modeling (GAM) by directional category was assessed to identify substantial changes in reflectance at boundaries of sand dune fields. Comparisons were made from 1985 to 2002, 2007 and 2014 and all models were assessed at 0.05 significance level (all significant models are in bold). The table contains (A) effective degrees of freedom, (B) F-value and (C) P-value of the GAM process for each directional category. The significant positive reflectance differences (dune creation) toward the south-east and east directions were observed across all three comparisons from 1985 to 2002, 2007 and, 2014. The negative reflectance differences indicating vegetation encroachment were only significant on the western dune boundaries across all three comparisons.
Table 5. The distance of sand dune creation (east and south-east) and woody vegetation encroachment (west) calculation from 1985 to 2002, 2007 and 2014.

| Duration     | Number of years | Sand dune creation (m year⁻¹) | Vegetation encroachment (m year⁻¹) |
|--------------|-----------------|--------------------------------|----------------------------------|
| 1985–2002    | 17              | 3.49                           | 7.11                             |
| 1985–2007    | 22              | 3.79                           | 5.66                             |
| 1985–2014    | 29              | 2.57                           | 4.77                             |
| Marginal means |                | 3.28                           | 5.85                             |

The table illustrates calculated distance of positive or negative reflectance difference was observed using Generalized Additive Modeling (GAM) technique for each pair wise comparison. The positive reflectance difference relationship indicates sand dune creation and the negative reflectance difference relationship indicates dense vegetation encroachment. The positive distance was calculated from zero (edge of the dune field) to a point where lower confidence limit crosses the main X-axis. The negative distance was calculated from zero (edge of the dune field) to a point where upper confidence limit crosses the main X-axis. More detailed illustration of distance calculation available in Figure S9. The calculation process was similar in each pair wise comparison and the marginal mean was calculated to obtain average of all three estimates.

Sand dune creation and vegetation encroachment

The main zones of sand movement into existing vegetation identified in the PCCD and GAM approaches were along the east and south-east edges of the sand dune fields. The rate of creation of new sand surfaces was 0.14 km² year⁻¹, a very slow process in comparison to total dune area (~349 km²) and open sand surface (~225 km²). Similarly, the GAM shows that positive reflectance difference moved at approximately 3.28 m year⁻¹ only on the south-east and east edges of the dune fields. The analysis of climate data support both the PCCD and GAM results regarding the influences of the wind regime on dune creation and vegetation encroachment. Winds toward the south-east to north-east directional range (winds from 220° to 310° directional range) were most common in the area at the end of the summer and the beginning of the fall (Fig. 7) in combination with low precipitation (Fig. 6) reflects the most potential drive to move sand. Carson and MacLean (Carson and MacLean 1986), stated that the Athabasca sand dunes were migrating to the north-east at a much lower rate of about 0.5 m year⁻¹. This difference likely reflects the spatial and temporal limitations of short-term field-based work to measure a slow process dependent on variable weather conditions.

Vegetation growth into the dunes between 1985 and 2014 mainly occurred at the west sides of the sand dune fields. The total area occupied by woody vegetation from 1985 to 2014 was 57.55 km² and the rate of change was 1.98 km² year⁻¹. This likely reflects reduced sand dune activity on the west side of dunes as the predominant sand dune movement was to the east. The GAM shows that the negative reflectance difference moved approximately 5.85 m year⁻¹. The exact mechanisms driving reductions in active sand movement on the west side of dune fields remain unclear. However, higher frequencies of wind toward the east and south-east directions in the summer may contribute to active sand movement opposite to west boundaries of the dune system. Coniferous tree spread in the west could be aided by either reduced wind-driven dune activity or declines in fire frequency. Active fire suppression is rarely attempted in this remote region, however, suggesting wind as the most likely mechanism. The rate of dune movement (creation of ~ 0.14 km² year⁻¹) is outweighed by the average loss of 1.98 km² year⁻¹ to forest succession, though these rates are very small relative to the total dune area (~349 km²). However, we observed an increasing rate of sand dune surface loss between 1985 and 2014, with a net area loss of 1.15 km² year⁻¹ between 1985 and 2002 and 1.85 km² year⁻¹ between 1985 and 2014. The total dune area lost to 2014 was 53.76 km², 20 percent of the total dune extent in 1985. It is not clear whether this loss pattern is transitory, or whether it may reflect larger climatic changes that favor stabilization of Athabasca sand dunes.

In summary, our goals were (1) to describe the physical environment of the Athabasca endemics, (2) estimate the distribution of each taxa and (3) to evaluate the potential impact of dune creation and forest encroachment on these populations. Understanding these factors are critical to evaluating the long-term viability and conservation status of these taxa, particularly the less abundant species. We evidence that the long-term dune stabilization processes are occurring, while currently abundant and widely distributed taxa may be at risk. This is likely due to a historical shift in wind patterns and associated movement of sand to the north-east to south-east directional range. Reduced dune activity favoring woody vegetation establishment is a significant long-term threat as the preferred habitat of the Athabasca taxa contracts. Development of higher resolution...
remote sensing strategies to more precisely model the extent of gravel pavements and wet inter-dune slacks using the spectral signatures of exposed gravel and sand surface soil moisture will be important to identify the most critical habitat elements in the landscape. Overall, our current analysis documents the long-term dynamics of this sand dune environment, and how those dynamics relate to the long-term security of the Athabasca sand dune endemic flora.

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### Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Figure S1:** Field survey sampling transect plan.

**Figure S2:** Work flow overview.

**Figure S3:** Sampling transect map of MacFarlane River dune field.

**Figure S4:** Sampling transect map of Thompson Bay, and William River dune fields.

**Figure S5:** Analysis of prediction errors and accuracies based on varying threshold probabilities.

**Figure S6:** Generalized additive modeling (GAM) results of directional sand movement analysis from 1985 to 2002.

**Figure S7:** Generalized additive modeling (GAM) results of directional sand movement analysis from 1985 to 2007.

**Figure S8:** Generalized additive modeling (GAM) results of directional sand movement analysis from 1985 to 2014.

**Figure S9:** Illustration of sand dune and vegetation movement distance calculation using generalized additive models (GAM).

**Table S1:** Habitat types identified during fieldwork in the Athabasca sand dunes following Lamb, Mischkolz (Lamb et al. 2011) and habitat types used in this study.
Table S2: Analysis of estimate uncertainty based on varying threshold probabilities.
Table S3: Iterative Self-Organizing Data (ISODATA) unsupervised classification statistics.
File S1: Support figures and tables. The file includes all supporting figures and tables.
File S2: Detailed methods. A detailed explanation of steps followed in all methods used in the study. 1) habitat/species distribution mapping, 2) bitemporal layer stack (BTLS), 3) the post-classification comparison change detection (PCCD) and 4) generalized additive modeling (GAM) approach to estimate directions and movement distances of sand dune and vegetation at dune boundaries.
File S3: 2009 Model Evaluation R script file. The file contains all detailed steps followed in habitat/species modeling procedure – 2009 data.

File S4: 2009 Species and reflectance original data file. The data file contains all information used in habitat/species modeling procedure – 2009 data.
File S5: 2010 Model Evaluation R script file. The file contains all detailed steps followed in habitat/species modeling procedure – 2010 data.
File S6: 2010 Species and reflectance original data file. The data file contains all information used in habitat/species modeling procedure – 2010 data.
File S7: 1985-2014 Dune dynamic analysis R script file. The file contains all detailed steps followed in the GAM procedure for sand dune creation and stabilization analysis.
File S8: 1985-2014 Reflectance data file. The data file contains all information used in the GAM procedure for sand dune creation and stabilization analysis.