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Regeneration vulnerability assessment for dominant tree species in the central interior of British Columbia

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Regeneration vulnerability assessment for dominant tree species throughout the central interior of British Columbia

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Abstract

The Intergovernmental Panel on Climate Change has stated that climate change is occurring at a faster rate than previously predicted. In response, the British Columbian Ministry of Forests and Range has recently developed the Future Forest Ecosystem Scientific Council to begin research into adapting forest and range management in response to climate change. To engage in adaptation, forest managers need to understand the potential response of species to predicted climate change. To provide this understanding we assessed the vulnerability and risk of the dominant tree species in the central interior ecosystems in British Columbia to climate change using the TACA model. The assessment identified mixed risk response both between species and ecosystems and between site types. *Pinus contorta* var. *latifolia*, *Picea mariana*, and *Populus tremuloides* were found to be quite resistant to climate change across all sites in which they typically occur within the study area with the exception of the southernmost (IDF) ecosystems. *Picea glauca* X *engelmannii* and *Betula papyrifera* were found to exhibit vulnerability on dry sites but resistance on mesic and moist sites while *Abies lasiocarpa* and *Populus balsamifera* ssp. *trichocarpa* exhibited resistance on moist sites throughout the region; except in the southernmost ecosystems. An increase in the establishment coefficients for *Pseudotsuga menziesii* var. *glauca* was modelled across the region though significant frost risk still occurred with the future ESSF and BWBS

ecosystems. The majority of species responded to modelled climate change favourably in the ESSF, BWBS, and the wet and cool SBS ecosystems; the exception being *Picea engelmannii*. *Picea engelmannii* was modelled to be at the highest risk to climate change. Species were affected in the ICH ecosystems due to a decline in winter chilling but establishment coefficients still remained sufficiently high. The findings from this study point to divergent species responses that could lead to changes in recruitment over time and eventually to changes in species dominance at the stand then ecosystem-level; however, edaphic conditions were found to exacerbate and mediate species responses. The mesic to moist sites within the majority of the region's ecosystems may offer managers the ability to continue management under a business as usual scenario whereas new policies may be required to ensure that dry (xeric to submesic) sites are able to be reforested successfully under climate change, particularly in the southernmost portions of the Central Interior. Further research is required to exam the interaction between changes in establishment potential with changes in species productivity, inter-species competition, and disturbance agents.

Keywords: Climate Change; Ecosystem; Vulnerability; Regeneration; Risk, Resilience

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Introduction

The Intergovernmental Panel on Climate Change (IPCC) Fourth Assessment Report stated the need for research into understanding the mechanisms that predispose physical, biological and human systems to irreversible changes as a result of exposure to climate and other stresses (Parry *et al.*, 2007). Parry *et al.* (2007) go on to argue the need for scientists to identify how close natural ecosystems are to ecological thresholds and what positive feedback loops might occur if these thresholds are exceeded. As a result, research needs to focus on the mechanisms that enhance system resilience or vulnerability so that the risk of irreversible change can be diversified through an understanding of ecosystem response to these thresholds. British Columbia's Ministry of Forests and Range (MOFR) has recently developed the Future Forest Ecosystem Scientific Council (FFESC) to begin adapting forest and range management in response to climate change. The initiative has outlined six objectives for adapting British Columbia's forest ecosystems (MOFR, 2008). The first two objectives relate to understanding the functional constraints for key species and ecological processes and how these species and processes may be altered over time as climate changes (MOFR, 2008). The objectives of the FFESC have been designed to facilitate our understanding of ecosystem processes and responses to climate change so that adaptation strategies can be developed that enhance ecological resilience and ecosystem services (MOFR, 2008). These provincial objectives are in line with the recommendations of the IPCC and support their assertion for the need to understand potential ecosystem responses to climate change.

Ecosystems are the basic units of nature, created by the interaction between living organisms and the abiotic components of the environment (Tansley, 1935). Changes in any biophysical component can alter the stable dynamic equilibrium that exists between biotic and abiotic components leading to the creation of new ecosystems (Tansley, 1935). Climate change is a stressor that will directly or indirectly influence the processes that influence both the formation and maintenance of ecosystems. A significant restructuring of the controlling variables and processes can shift an ecosystem to a new stable state (Gunderson *et al.*, 2002). The ability of an ecosystem to recover from natural disturbances and management actions or persist under changes in climate is referred to as ecological resilience (Holling, 1996).

The structure of an ecosystem is driven by species-level responses to change in the environmental factors that determine a species' distribution and abundance. The distribution of a species is defined by competition, dispersal, and the distribution of environmental conditions in space and time (Pulliam, 2000). A common concept that used to explain species presence and absence over time and space is the niche concept (Guisan & Zimmermann, 2000). A species' niche varies in breadth depending on environmental factors (i.e. fundamental or Grinnellian niche) and biotic interactions (i.e. realised niche) (Hutchinson, 1957; Schoener, 1989; Pulliam, 2000). Grubb (1977) identified that a plant's niche is comprised of four component niches: habitat, life-form, phenological and the regeneration niche. Grubb (1977) defined the habitat niche as a "plant's address" that occurs within a set of environmental limits that can be tolerated. The life-form niche relates to a species' size, structure and productivity while the

phenological niche refers to the pattern of seasonal development that a plant exhibits (Grubb, 1977). The regeneration niche is defined by Grubb (1977) as the range in which a species has a high chance of success in the replacement of a mature individual by new individual. Grubb (1977) stated that the regeneration niche comprises elements of the habitat, life-form and phenological niches. The processes and events that occur during the regeneration phase of natural communities can play a key role in community composition and may affect species diversity and promote species coexistence in environments that are homogeneous at the adult plant scale (Grubb, 1977). Florence (1964) stated that an ecosystem is an expression of environmental pressures and that change in communities are sensitive and predictable to changes in the edaphic environment. Consequently, environments that are effectively homogeneous at the scale of the adult can be patchy at the seed or seedling scale (Battaglia, 1997). Thus the distribution and abundance of species may reflect the breadth of a species regeneration niche in interaction with the environmental conditions at the time of establishment. The breadth of a species regeneration niche is typically narrower than in a species habitat, reproductive and dispersal niches (McKenzie *et al.*, 2003a; Young *et al.*, 2005). Most species are most sensitive to changes in the environmental within the early life stages of their regeneration niche (Grubb, 1977; Morin & Lechowicz, 2008). This is supported by Ibanez *et al.* (2007) who found that germinants and seedlings of temperate species in the southeast USA were affected by minor changes in climate which had no affect on adult tree populations. Zimmerman *et al.* (2009) also highlighted the increased sensitivity of species during regeneration to climatic extremes. Limitations in resource availability (moisture, nutrients, light, etc) are key factors that limit the breadth of this niche (Grubb,

1977; Fagerström & Ågren, 1999). In particular, soil moisture can affect a species ability to establish or grow (Pulliam, 2000). Phenology is also an important determinant of a species regeneration niche through its impact on flowering and growth in interaction with frost and drought (Grubb, 1977; Chuine & Beaubien, 2001; Morin *et al.*, 2007).

To establish the vulnerability of ecosystems to climate change we need to consider the response of individual species. Organisms in assemblages can have differential responses to the same climatic conditions/ or disturbance events (Walker, 1989). The magnitude of divergent responses between species is driven by their unique physiology, demographics and life-cycle characteristics (Walker, 1989). These divergent responses suggest that an ecosystem can be composed of species that are resilient to environmental change and those that are not. Thus, a species can be resilient, but the ecosystem may not, and vice versa. Species are most vulnerable to changes in environmental conditions in the regeneration phase since it is the most critical phase for their survival (Bell, 1999).

Understanding species vulnerability at this stage is therefore an important step if we are to determine where, and what, adaptation strategies are to be incorporated into long-term forest planning and risk management in relation to climate change (Nitschke & Innes, 2008c). In this study, we seek to understand the response of the dominant tree species within the central interior ecosystems of British Columbia (BC) to predicted climate change.

Study Area

Central Interior

The Central Interior Study Region (CISR) is approximately 15.5 million ha and occupies about 16% of the province of British Columbia. British Columbia is classified into 14 broad ecosystems referred to as biogeoclimatic (BEC) zones (Meidinger and Pojar, 1991). The CSIR contains six forested BEC zones: the Sub-Boreal Spruce (SBS), Sub-Boreal Pine and Spruce (SBPS), Interior Cedar Hemlock (ICH), Interior Douglas-Fir (IDF), Boreal White and Black Spruce (BWBS), and Engelmann Spruce-Subalpine fir (ESSF) ecosystems which are further sub-classified into 27 subzones and variants.

Figures 1 to 3 illustrate the CISR region (Fig 1) and the area occupied by each BEC zone (Fig 2) and their respective subzones and variants (Fig 3). The dominant BEC zone within the region is the SBS zone which considered a transitional zone between the montane forests of Douglas-fir (*Pseudotsuga menziesii*) in southern BC, the boreal forests of northern BC and the subalpine forests that occur at higher elevations within the central interior (Pojar *et al.*, 1982). The SBS has a continental climate that is characterised by seasonal extremes in climate with cold, snowy winters and warm, moist summers (Meidinger *et al.*, 1991). The ICH zone occurs at low to middle elevations (100 to 1000 m) and has an interior, continental climate that produces cool wet winters and warm dry summers (Ketcheson *et al.*, 1991). The ESSF occurs at elevations between 900 and 1700 m and is characterised by a cold, moist and snowy continental climate with short and cool growing seasons and long and cold winters (Coupé *et al.*, 1991). The BWBS is dominated by a northern continental climate characterised by long, very cold winters and short growing seasons (DeLong *et al.*, 1991). The IDF has a continental climate which is

characterised by warm, dry summers and cool winters that creates a long growing season (Hope *et al.*, 1991). The IDF is dominated by Douglas-fir. The SBPS has a continental climate and is characterised by cold, dry winters and cool, dry summers with frosts common throughout the growing season (Steen & Demarchi, 1991).

The dominant species within the CISR are: interior spruce (*Picea engelmanni* X *glauca*), Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*); black spruce (*Picea mariana*), lodgepole pine (*Pinus contorta* var. *latifolia*), Douglas-fir (*Pseudotsuga menziesii*), trembling aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*) and black cottonwood (*Populus balsamifera* ssp. *trichocarpa*). Within the SBS portion of the CISR the climax forests are dominated by interior spruce (*Picea engelmanni* X *glauca*), subalpine fir (*Abies lasiocarpa*); black spruce (*Picea mariana*) is also present.

Lodgepole pine (*Pinus contorta* var. *latifolia*) is the dominant fire climax species. Early seral stands are dominated by lodgepole pine and trembling aspen (*Populus tremuloides*), with paper birch (*Betula papyrifera*) common on rich-moist sites. Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) occurs as a long-lived seral species, and black cottonwood (*Populus balsamifera* ssp. *trichocarpa*) is a minor component that occurs within moist site types and in riparian areas and floodplain forests (Pojar *et al.*, 1982).

Within the ESSF, subalpine fir and Engelmann spruce dominate the climax forests with lodgepole pine as the dominant fire climax/ seral species (Coupé *et al.*, 1991). Deciduous species are uncommon in the ESSF and Douglas-fir is absent from the ESSF zones within the CISR. Within the SBPS, lodgepole pine is the dominant species with interior spruce and trembling aspen common on mesic to moist sites (Steen & Demarchi, 1991).

Douglas-fir, subalpine fir, black spruce, and black cottonwood are occasionally found within the SBPS (Steen & Demarchi, 1991). In the BWBS white spruce (*Picea glauca*), black spruce, lodgepole pine, paper birch, subalpine fir, trembling aspen, and balsam poplar (*Populus balsamifera*) are the most common species (DeLong *et al.*, 1991). Within the ICH all the dominant species listed above occur. Interior spruce (and other spruce hybrids/ species) and subalpine fir along with black cottonwood form edaphic climaxes while lodgepole pine, Douglas-fir, trembling aspen and paper birch are common seral species; black spruce also occurs in poor-moist to wet habitats (Ketcheson *et al.*, 1991). Though western red cedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) are common in the ICH zone they are primarily absent from the remainder of the CISR and were therefore not included in this study.

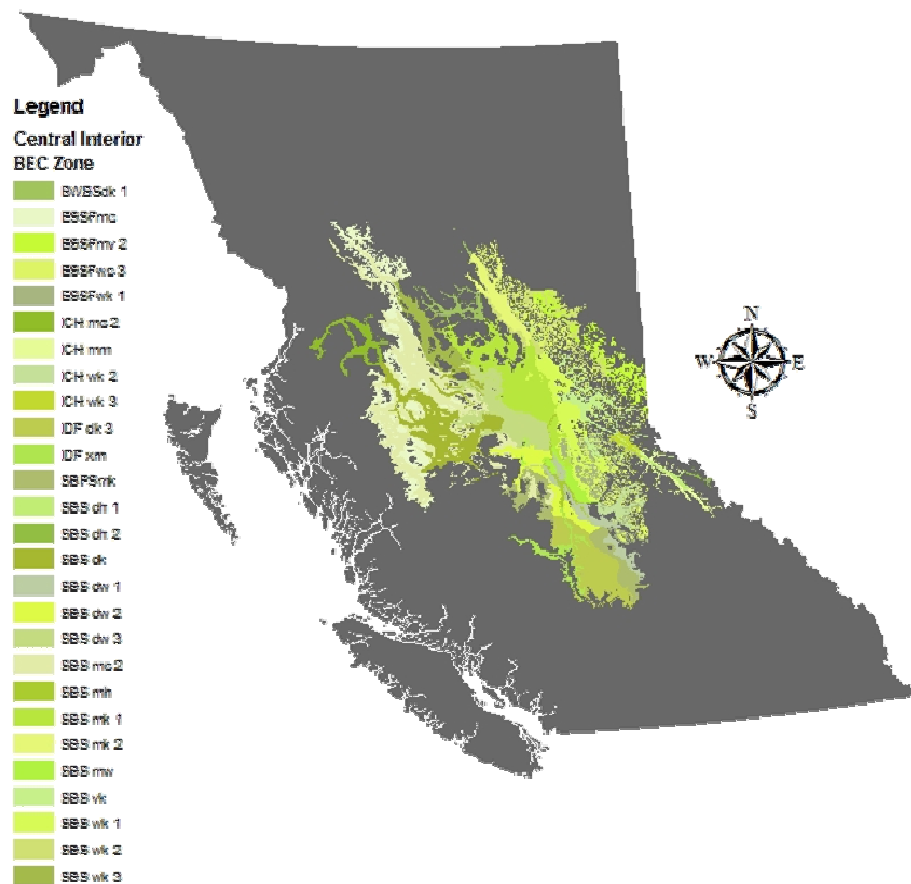


Fig. 1: Central Interior Study Region within British Columbia and ecosystem composition at the BEC zone/ subzone/ variant level.

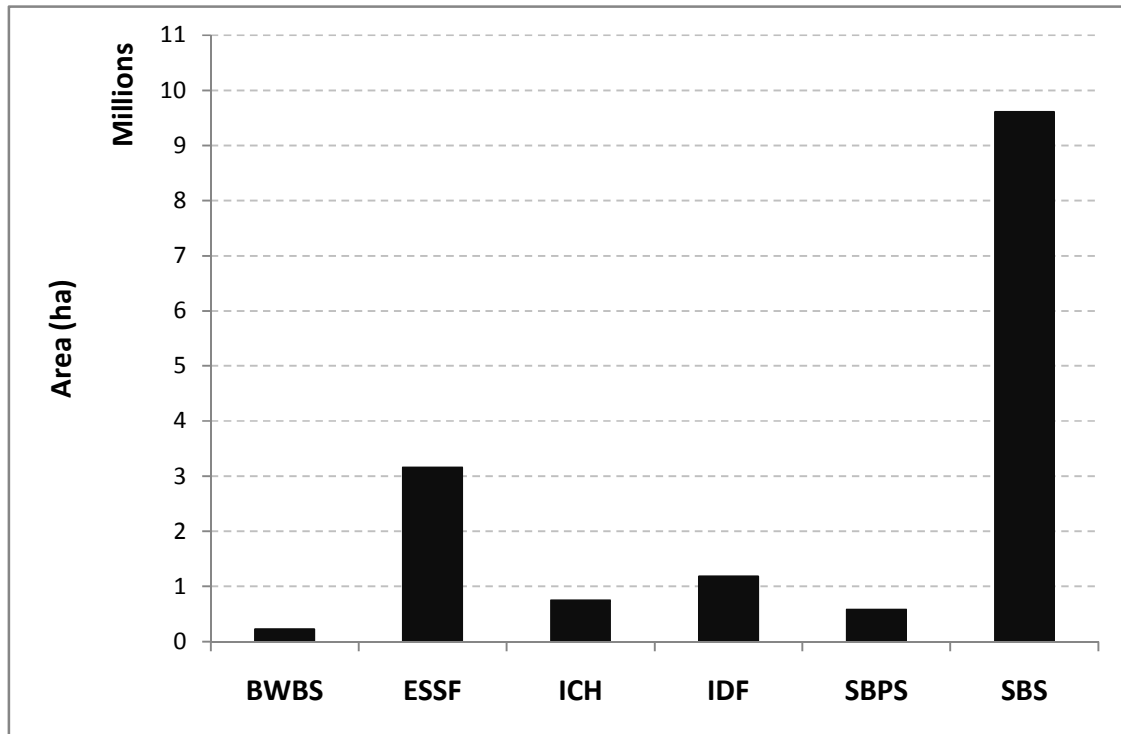


Fig. 2: Area occupied by each BEC zone in CISR

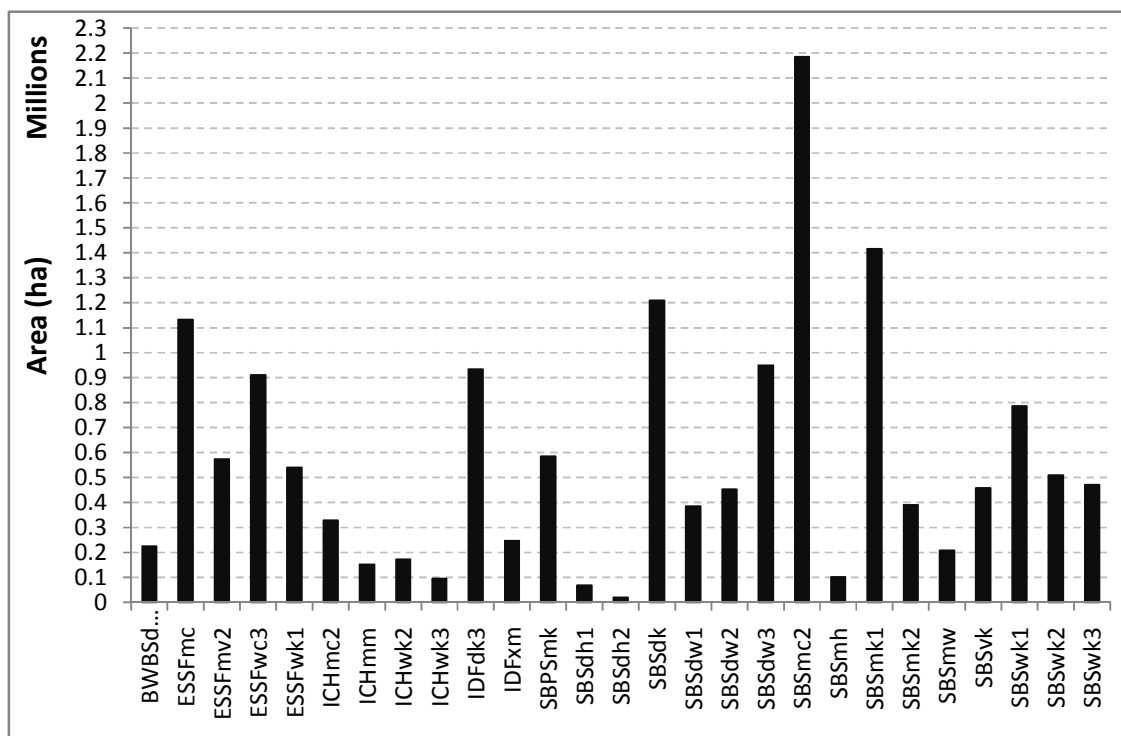


Fig. 3: Area occupied by each BEC subzone and variant in CISR

Methods

Vulnerability assessments are recommended as the best method for assessing potential climate change impacts (IPCC 1998; Lemmen & Warren 2004). Using this approach we have analysed the possible effects that predicted climate change will have on the vulnerability of the dominant tree species in the CISR. The research presented in this report follows and expands on the approach used by Nitschke & Innes (2008a; 2008c) to model species and vulnerability to changes in climate in the Southern Interior of British Columbia, Canada.

Tree species that dominate or are common across the CISR were selected for analysis. Nine species were selected [see Table 1 - binomials follow Farrar (1995)]. Species were selected based on the descriptions of ecosystems in the Land Management Handbook series of field guides on site identification and interpretation of forest ecosystems and Ecosystems of British Columbia (Meidinger & Pojar, 1991).

Table 1: Species selected for assessment of species vulnerability within the CISR

Common Name	Scientific Name
Broadleaf Species	
paper birch	<i>Betula papyrifera</i> Marsh.
black cottonwood	<i>Populus balsamifera</i> ssp. <i>trichocarpa</i> (Torr. & Gray) Brayshaw
trembling aspen	<i>Populus tremuloides</i> Michx.
Conifer Species	
subalpine fir	<i>Abies lasiocarpa</i> (Hook.) Nutt.
Engelmann spruce	<i>Picea engelmannii</i> Parry ex Engelm.
interior spruce	<i>Picea glauca</i> (Moench) Voss x <i>engelmannii</i> Parry ex Engelm.
black spruce	<i>Picea mariana</i> (Mill.) BSP
lodgepole pine	<i>Pinus contorta</i> Dougl. ex Loud. var. <i>latifolia</i> Engelm.
Douglas-fir	<i>Pseudotsuga menziesii</i> var. <i>glauca</i> (Beissn.) Franco

The Ecological Model

The ecological model, TACA (Tree And Climate Assessment) (Nitschke & Innes 2008a), was modified and parameterised for use in the ecosystems of the CISR. TACA is a

mechanistic species distribution model (MSDM) that assesses the probability of species to be able to regenerate, grow and survive under a range of climatic and edaphic conditions. TACA conducts a scenario analysis to determine an establishment coefficient (probability of establishment) for a species across a range of climate scenarios. The modelling of establishment (i.e. presence/ absence) reflects the regeneration niche of a species, because presence is directly related to establishment, providing a modelling approach that is robust to life-history changes in species (McKenzie *et al.* 2003a). . The original TACA model developed by Nitschke & Innes (2008a) was modified to incorporate a frost free period mechanism. Hamann & Wang (2006) found that the annual number of frost days had a significant interaction with observed species ranges in BC. The phenology component of TACA was also improved to increase the interaction between chilling, heat sum accumulation, frost, and budburst based on Bailey & Harrington (2006). The new phenology component integrates the obtainment of a species chilling requirement with the accumulation of it heat sum which then interacts with frost events that delay bud burst and/ or causes frost damage after bud burst occurs. The soil moisture function was upgraded to the full Penman-Monteith equation (McNaughton & Jarvis 1983; Waring & Running 1998) which is driven by estimates of daily solar radiation based on calculations from Bristow & Campbell (1984) and Ferro Duarte *et al.* (2006). In addition the soil component of TACA was expanded to allow for three different soil types (texture, coarse fragment content and rooting depth) to be run simultaneously allowing for the representation of multiple edaphic conditions across the resource gradient used in this study. Snowfall, snow accumulation, and snowmelt are also included in this version of the model. Snowfall and accumulation is tracked in snow

water equivalent (mm). Snow melt utilises the snow melt model from Brubaker *et al.*

(1996). A diagram of the modified TACA model and information flow is presented in

Figures 4a and 4b.

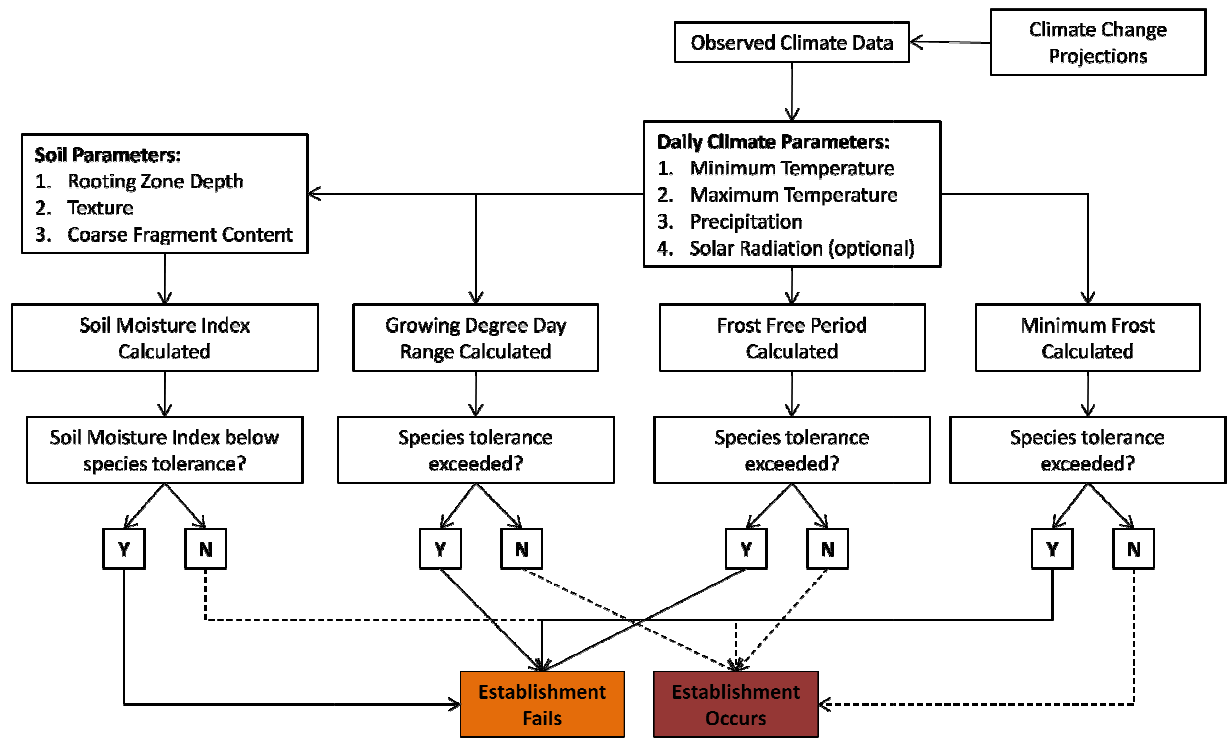


Fig 4a: Flow diagram of habitat niche elements within TACA that determines species establishment

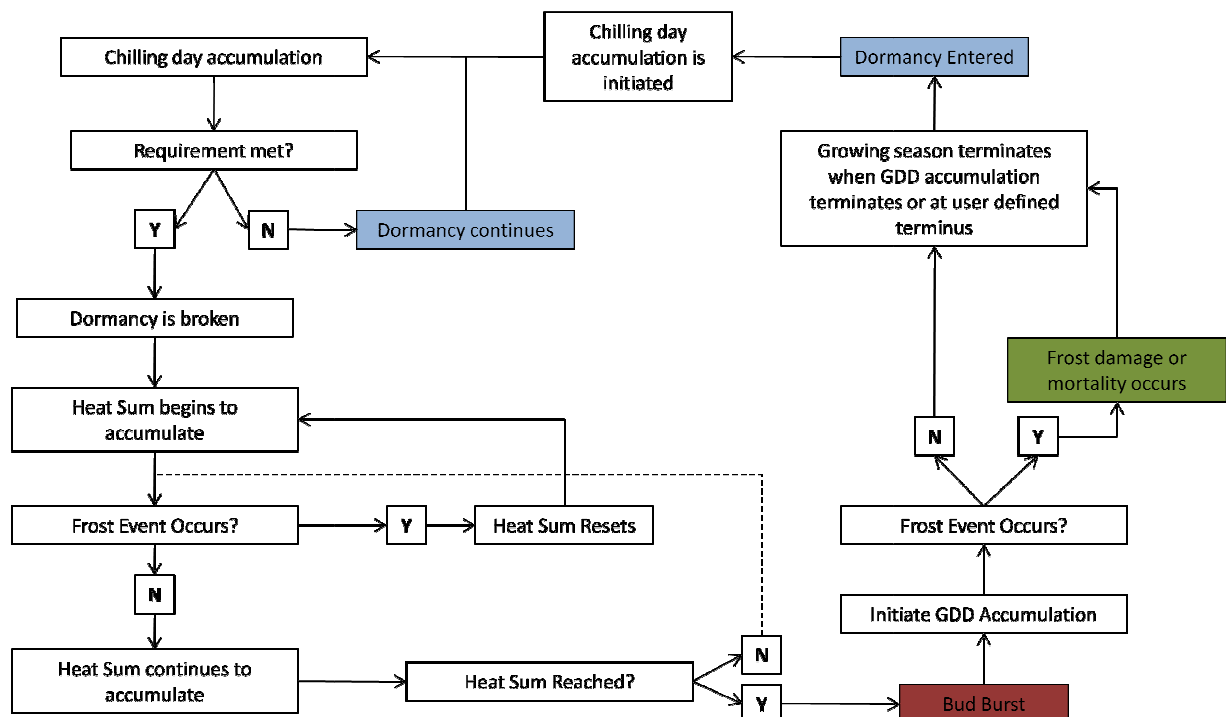


Fig 4b: Flow diagram of phenological niche elements within TACA that determines initiation of species growth and occurrence of frost damage

Species Parameters

Species-specific parameters used in TACA (see Table 2) follow Campbell & Sugano (1975), van den Driessche (1975), Campbell & Ritland (1982), Bonan (1989), Burns & Honkala (1990); Urban *et al.* (1993), Burton & Cumming (1995), Cumming & Burton (1996), Zolbrod & Peterson (1999), McKenzie *et al.* (2003a; 2003b), McKenney *et al.* (2007) and, Nitschke & Innes (2008a)

Table 2: Species-specific parameters for assessing species regeneration potential within the SBS zone of the Bulkley Valley

Broadleaf Species	T_{base}¹	BB¹	CR¹	Min T¹	Drought¹	Frost¹	GDD Min¹	GDD Max¹	Frost Days¹
paper birch	3.7	231	77	-80	0.30	0.9	237	4122	285
black cottonwood	4.6	175	70	-60	0.13	0.5	258	5263	295
trembling aspen	3.5	189	70	-80	0.40	0.9	227	4414	284
Conifer Species	T_{base}¹	BB¹	CR¹	Min T¹	Drought¹	Frost¹	GDD Min¹	GDD Max¹	Frost Days¹
subalpine fir	2.6	119	60	-67	0.20	0.9	198	5444	270
Engelmann spruce	3.1	145	49	-45	0.20	0.9	74	1344	335
interior spruce	2.9	146	45	-58	0.27	0.9	139	3331	305
black spruce	3	123	56	-69	0.30	0.9	144	3060	305
lodgepole pine	2.9	116	63	-85	0.42	0.9	186	3374	285
Douglas-fir	3.4	255	56	-37	0.50	0.5	177	3261	300

¹: T_{base} (°C): species-specific threshold temperature for initiating physiological activity, BB (Heat Sum):

heat sum required to initiate bud burst (BB), CR (weeks): Number of chilling days required for chilling requirements to be achieved, Min T (°C): a temperature below this threshold is considered fatal to a tree, Drought (threshold: % of season which can be survived under a water deficit), Frost (presence probability modifier), GDD Min & GDD Max (degree days): minimum growing degree days required for survival and maximum growing degree days that limits growth through heat stress, Frost days (maximum number of frost days that can be tolerated in a year)

Soil Parameters

The soil-water component of the model were parameterised from plot data from the Biogeoclimatic Ecosystem Classification Database (BECdb) provided by the Ministry of Forests and Range. Plot data that contained rooting zone depth, soil texture and coarse fragment percentage classes for the relevant ecosystems within the study region where analysed to calculate the average available soil water holding capacity and field capacity in TACA for three site types: dry-poor, mesic-medium, and moist-rich. Table 3 summarises the typical soil conditions

Table 3: standard range of soil parameters used in study. Actual soil moisture regime is dependent on ecosystem while relative soil moisture regime is related to edatopic grid co-ordinates. Poor refers to a soil nutrient regime of B, Medium to C and rich to D on the edatopic grid.

Soil Parameters	Values		
Site Type	Dry-Poor	Mesic-Medium	Moist-Rich
Relative Soil Moisture Regime	1-2	3-4	5-6
Actual Soil Moisture Regime	VD-SD	SD-M	F-M
Soil Texture	S-LS	SL-L	L-SiL-SiCL
Soil Rooting Zone Depth (m)	0.25 – 0.35	0.30 – 0.50	0.20- 0.45
Coarse Fragment %	0.37 - 0.69	0.25- 0.55	0.06 - 0.34

The soil nutrient regime of a site can influence species ability to establish. To incorporate the effect of nitrogen on species establishment the tolerance of species to nitrogen levels on a site, as classified by Klinka *et al.* (2000), were used to develop modifiers for each species. The modifiers were used to adjust the establishment coefficients of each species for each site type. Table 4 summarises the nitrogen tolerance modifiers for each species.

Table 4: nitrogen tolerance modifiers used in study

Species	Low	Medium	High
Black Cottonwood	0.25	0.5	1.0
Lodgepole Pine	1.0	1.0	0.5
Subalpine Fir	1.0	1.0	0.75
Black Spruce	1.0	0.5	0.1
Engelmann Spruce	1.0	1.0	0.5
Paper Birch	0.5	1.0	0.75
Douglas-fir	0.75	1.0	0.75
Trembling Aspen	0.75	1.0	0.75
Interior Spruce	0.75	1.0	0.75

Climate Parameters

Climate inputs to TACA are: minimum temperature, maximum temperature and precipitation on a daily time step for one year. Climate data from 63 weather stations were used; Figure 5 summarises the number of stations per ecosystem. Daily weather data that fell within the years 1950 to 2003 for each location were analysed using a rank

and percentile test. Based on the rank and percentile test 10 historical years of climate data were selected and used as the historical climate scenarios in the analysis. The 10 years of data represent the 90th, 75th, 50th, 25th, and 10th percentiles for both observed annual precipitation and mean annual temperature. Duplicity between temperature and precipitation scenario selection was resolved using an annual heat-moisture index metric $[(\text{Mean Annual Temperature} + 10) / (\text{Precipitation} / 1000)]$ to select additional years from the climate distribution not covered by the initial selection criteria. For certain ecosystems only one weather station existed with less than 10 years of data so Monte Carlo techniques were used to sample the probability distributions of each daily variable to create ranges of change in order to generate additional scenarios (Nitschke & Innes 2008b). Additional generated weather scenarios from each station were then combined with the observed data scenarios to provide the 10 climate scenarios. The selected historical climate scenarios were used as the foundation for developing different climate change scenarios that incorporate daily climate variation. Bürger (1996) stated that incorporating daily climatic variation is important for improving the realism of climate change scenarios. The incorporation of extreme climate years is also important as species distributions are influenced by climatic extremes (Zimmerman *et al.*, 2009). The methodology also allows for the variability in climate conditions caused by the Pacific Decadal Oscillation (PDO), for example, to be incorporated into the study. Mantua *et al.* (1997) identified that from 1946 to 1977 the PDO was in a cool phase and from 1977 in a warm phase. During the warm PDO phase climate within western North America are typically 0.5 °C warmer and 10 % drier than in the cool phase (Mantua *et al.*, 1997). The scenarios with below average temperature conditions above average precipitation can

therefore represent the cool phase of the PDO and scenarios with above average temperature and below average precipitation can represent the warm phase of the PDO.

A direct adjustment approach (Wilks, 1999; Hamann & Wang, 2006) was used to create climate change scenarios from the selected historical climate data and global climate model (GCM) predictions for each location within the study region. Historical climate records for the 63 climate stations that represent the CISR were employed. The approach involved adjusting the weather station records using the predicted outputs from a GCM (Wilks 1999; Wang *et al.* 2006). A direct adjustment approach was used by Hamann & Wang (2006) and Nitschke & Innes (2008a) to model species response to predicted climate change. The predictions for changes in temperature and precipitation for each month from each climate change scenario were applied to the weather stations located in each ecosystem. Changes in temperature were increased by the predicted amount while changes in precipitation were multiplied by a factor that represented a percent change in that variable (ex. 0.92 or 1.12). These changes were applied on a month-by-month basis to create a daily time series of weather that represented the local variation, along with monthly variation of the GCM predictions.

Three different GCMs were used, the Canadian GCM3 (Flato et al. 2000), CSIROmk3b, and Hadley CM3 models (Johns et al. 2003). The Hadley model was found by Bonsal et al. (2003) to be the best GCM for predicting historic temperature and precipitation in BC and the CGCM and CSIRO models to be robust enough for use as well. The regional climate change predictions for the CISR were obtained from the Pacific Climate Impacts

Consortium (2009). Multiple climate scenarios were generated following Nakicenovic *et al.* (2000), who argued that due to the large amount of uncertainty regarding future climate change, multiple scenarios that span a range of possible future climates should be adopted. The Intergovernmental Panels SRES emission scenarios A1B, A1F1, and B1x were used to represent an ensemble of future climate conditions (Nakicenovic et al. 2000). The scenario-specific and ensemble values of these scenarios are presented in Table 5. Each ensemble represents three climate scenarios.

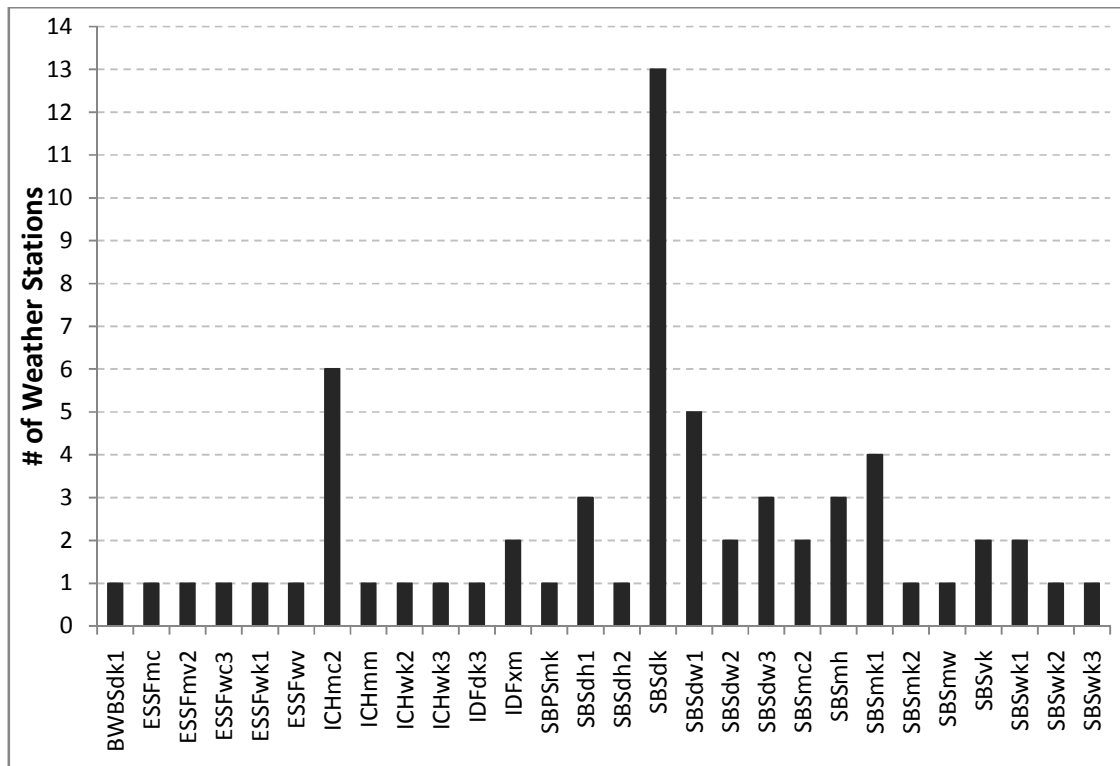


Fig 5: Number of suitable weather stations within each ecosystem used in the study. The ESSFmc and SBSwk3 scenarios required climate generation to augment observed data.

Table 5: Scenario-specific predictions and average annual predicted climate change by time slice in the CISR based on ensemble scenarios of predicted change

Climate Scenarios	Mean Annual Temp. (°C)	Autumn-Winter Temp. (°C)	Spring-Summer Temp. (°C)	Autumn-Winter Precipitation (%)	Spring-Summer Precipitation (%)
2020s-B1x ⁱ	1.4	1.7	1	6	8
2020s-B1	0.44	0.34	0.53	6	4
2020s-B11	1.15	1.2	1.1	7	-2
2020s-A1B	0.7	0.6	0.9	6	1
2020s-A1Bx	1.4	1.6	1.2	7	6
2020s-A1F1	1.14	1.05	1.23	3	-3
2050s-B1x	2.1	2.4	1.7	11	8
2050s-B1	1.3	1.35	1.26	8	1
2050s-B11	1.7	1.5	2	14	3
2050s-A1Bx	2.6	3	2.2	15	12
2050s-A1B	1.4	1.6	1.2	9	6
2050s-A1F1	2.3	2.2	2.5	3	-5
2080s-B1x	2.3	2.7	1.9	17	12
2080s-B1	1.6	1.8	1.5	11	2
2080s-B11	2.6	2.1	3	21	-3
2080s-A1Bx	3.2	3.6	2.7	19	14
2080s-A1B	2.2	2.3	2.1	12	11
2080s-A1F1	3.7	3.68	3.73	3	-7
Ensemble Scenarios					
2020s-1 ⁱⁱ	0.98	1.03	0.93	6	3
2020s-2	1.09	1.07	1.10	5	1
2050s-1	1.70	1.74	1.66	11	4
2050s-2	2.10	2.23	1.96	9	4
2080s-1	2.18	2.21	2.15	16	3
2080s-2	3.0	3.18	1.83	11	6

ⁱ: CGCM3 = A1Bx & B1x; CSIROmk3b = A1B & B1; HADCM3 = B11 & A1F1

ⁱⁱ: -1= B1 scenarios; -2= A1 scenarios

Replication and Analysis

Replication was achieved through the use of multiple climate change scenarios (n=18) and multiple weather stations where possible (n =1 to 13; see Fig. 5). Due to the lack of replication in many of the ecosystems a rigorous statistical analysis was impossible.

Single factor ANOVA was used to test if the change in establishment coefficients under climate change was significant however these results should be treated with caution and as such are being use to quantify the degree of risk a species is at. Because the TACA model provides a probabilistic value which follow a binomial distribution the results were transformed using the arcsin transformation to make the results representative of a normal distribution. A more thorough investigation of the ecosystems where a high number of weather stations occur would allow for statistical tests to be applied in a more meaningful manner and this is the subject of further research at this time.

Measuring Risk to Climate Change

Risk is typically defined as the probability and severity of adverse effects (O’Laughlin 2005). Haimes (1998) describes risk as having two components; one real (consequence) and one imagined (probability). In the context of climate change, risk has been defined as a function of hazard and vulnerability ($\text{Risk} = \text{Hazard} \times \text{Vulnerability}$) (Brooks et al. 2005). A hazard is defined as the cause of an adverse effect (O’Laughlin 2005). Vulnerability is defined as the degree to which a system or system component is susceptible to sustaining damage from a hazard (Turner et al. 2003). This vulnerability-based definition of risk is supported by the Intergovernmental Panel on Climate Change (IPCC) (1998) as the best definition for assessing climate change as it allows for the assessment of system vulnerabilities rather than expected impacts. To calculate species risk the following equation was developed:

Risk = Hazard X Vulnerability; where,

Hazard = $\sum AR/N$; and,

Vulnerability = minimum[AR]; where,

AR = adverse (i.e. negative) response to climate scenario in comparison to baseline

N= number of climate scenarios

Minimum [AR] = the most adverse response observed/ modelled

One of the limitations of the TACA model is the a-spatial design. To help overcome this limitation, the results for each species were integrated in ArcGIS 9.2 (Environmental Systems Research Institute, 2006) using a shapefile of the Biogeoclimatic ecosystem classification for the study area. Using the results from TACA, the risk to climate change for each species within each ecosystem was mapped for each site type. Unfortunately a single risk map that incorporated all site types was not possible due to incomplete data coverage of sites series classifications across the study area. If a comprehensive dataset becomes available such a risk map can easily be generated.

The following classification was used in the analysis to map and define risk:

1. Zero or positive response: no risk
2. Negative response: $>1 < 10\%$: low risk
3. Negative response: $\geq 10\% < 20\%$: medium risk (p value ≤ 0.30 to 0.05)
4. Negative response: $\geq 20 < 30\%$: high risk (p value ≤ 0.05)
5. Negative response: $>30\%$: very high risk (p value ≤ 0.001)

Results

At the ecosystem-level (Fig. 7) species response was greatest on site type 1 (dry-poor) followed by site 2 (mesic-medium) and site 3 (moist-rich). The IDFdk3 is the ecosystem that was modelled to have the highest risk to future climate change with every species exhibiting a negative risk response on each site type. The IDFxm, ICH and warmer and drier SBS ecosystems were also found to exhibit mixed degrees of risk. The BWBS, ESSF and wet and cool SBS zones exhibited the lowest degree of risk response at the ecosystem-level though in the ESSF species-specific responses point towards a different risk profile.

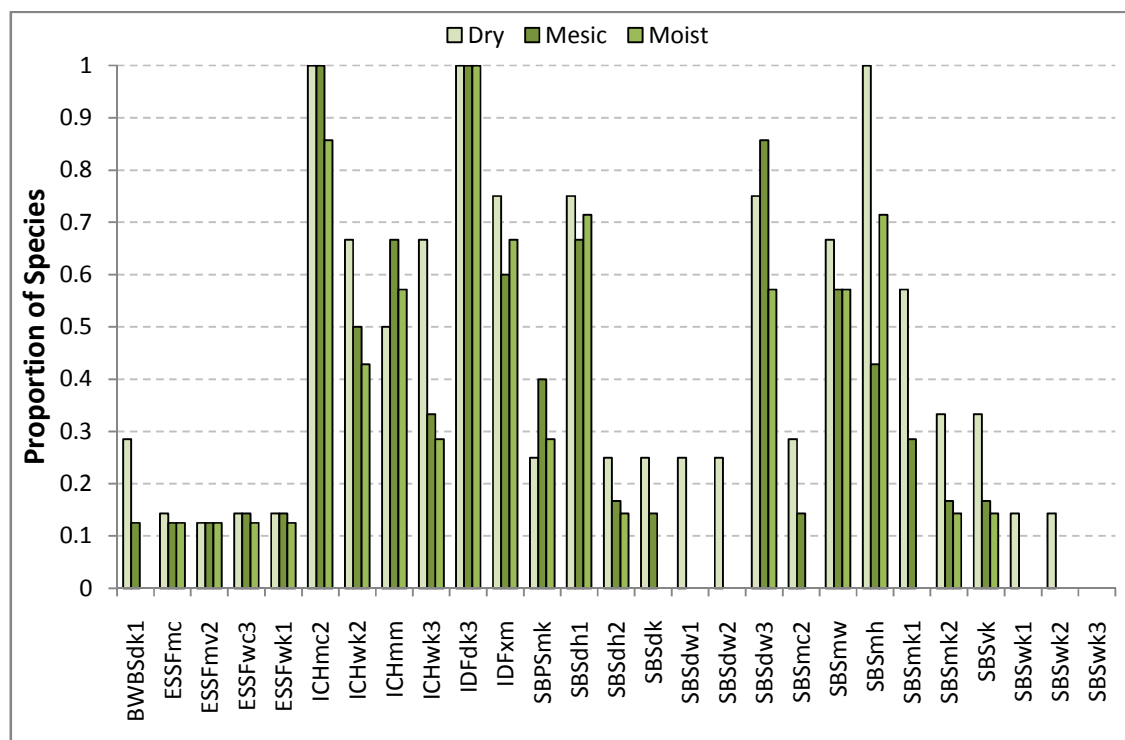


Fig 7: Proportion of species within each ecosystem exhibiting a low to high risk response to climate change across study area

Overall species were found to respond individually and have divergent responses within and between ecosystems. Figures 8 to 25 summarise the risk response profiles for each species and illustrate the risk profile spatially. Each species will be discussed separately. Individual species responses to each climate change scenario except the 2020s are provided in Appendix A. The 2020s were excluded for clarity and also because the responses across all species and sites were not discernable in any meaningful manner from the observed climate conditions.

Black cottonwood exhibited a variable risk response across the CISR (Figs 8 & 9). Since black cottonwood does not occur or is used currently on dry sites no risk was calculated though the modelling suggested high and increasing drought risk if utilised. On mesic sites the field guides identified that black cottonwood can occur on mesic sites in the BWBSdk1, IDFd3 and ICHmc2. Under mesic conditions, black cottonwood exhibited a positive response in the BWBSdk1 and significant risk responses in the ICHmc2 and IDFd3. Black cottonwood can occur on moist sites across the CISR ecosystems and it is on these sites that a variable risk response was identified. In the IDFd3 and IDFx, significant risk responses ($p \leq 0.05$) were modelled to occur under future climate change in the 2050s. Black cottonwood was classified at low risk across the ICH ecosystems and in three of the 15 SBS ecosystems. This species responded positively in 16 of the ecosystems with significant changes ($p \leq 0.05$) occurring in BWBSdk1, in all ESSF zones, in the SBSmk2 and SBSwk3, and finally in the SBPSmk. The positive response across these ecosystems was attributed to the reduction in growing season frosts

experienced by this species. Within the ICH ecosystems, in particular the ICHmc2, the lack of winter chilling became an increasingly important factor by the 2080s.

In ecosystems where the species exhibited neutral behaviour the predicted increase in autumn, winter and spring precipitation was sufficient enough to overcome a decline in summer precipitation in a majority of the climate scenarios on the moist sites and frosts became less limiting to black cottonwood.

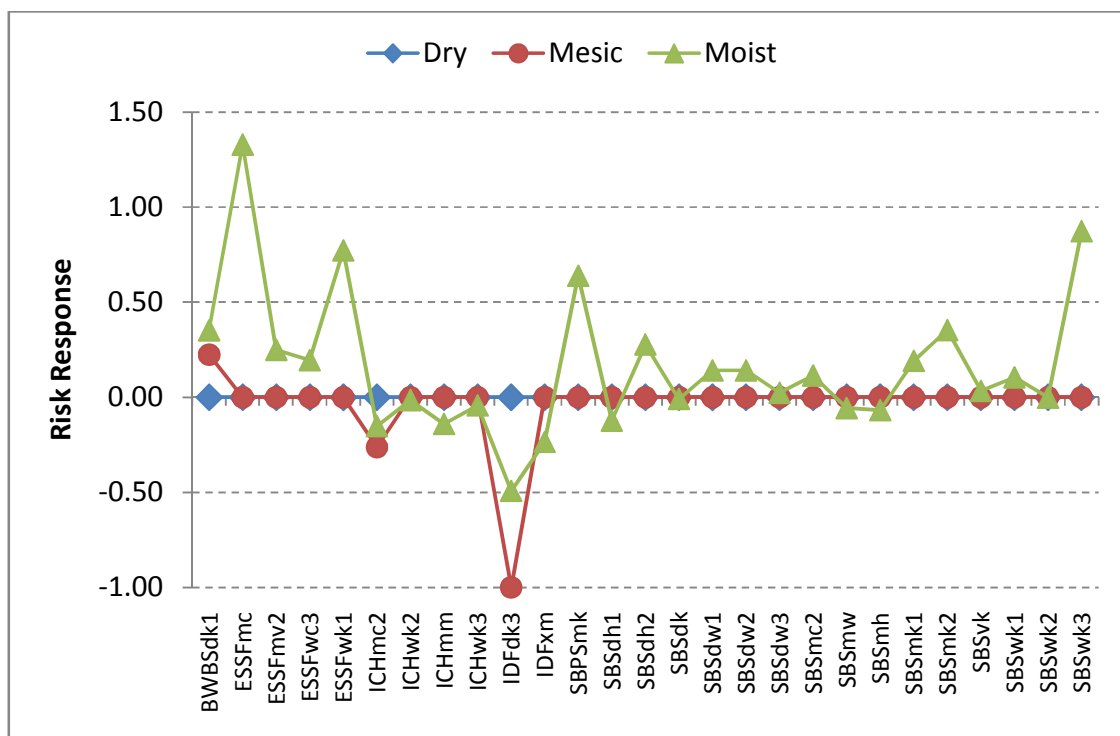


Fig 8: Risk response curve for black cottonwood across central interior study area

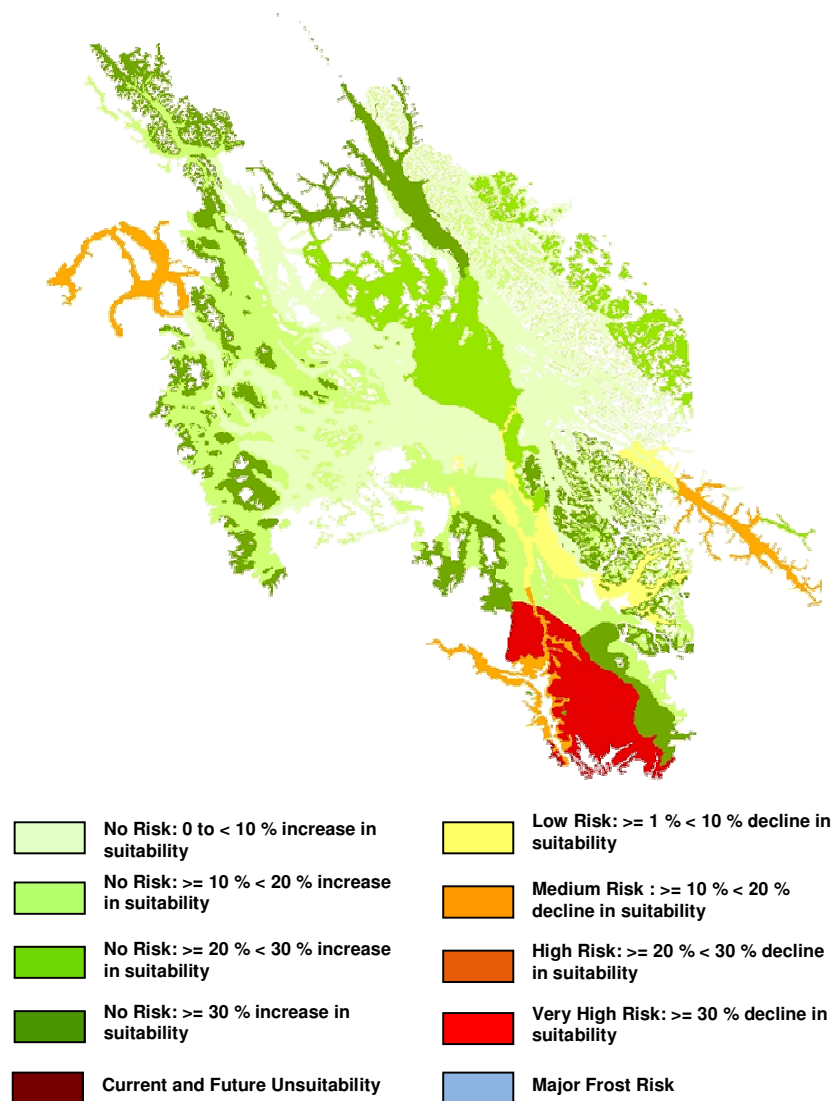


Fig 9: Risk map for black cottonwood on moist sites across central interior study area

Lodgepole exhibited a fairly static risk response across the CISR (Figs 10 and 11). On dry sites lodgepole pine was found to exhibit its highest risk on dry sites in the IDF zones and in the ICHmc2. In the IDFdk3 lodgepole pine shows a medium risk response across all sites. None of the risk responses were significant however but risks to drought in these systems may still impact this species in the future, particularly its productivity. The species establishment coefficients for lodgepole pine in Appendix A highlight the high

degree of suitability that this species maintains across a range of climate change in the CISR. Interestingly, lodgepole pine exhibited a negative response in the SBSdw3 (see Figs 10 and 11) which lead to the classification of low risk. This risk response, which is shared by many of other species in this ecosystem, is the consequence of an increase in frost damage that occurred under the 2050s-1 scenario. Under this scenario, the predicted warming increased the growing season length (early bud flush, later cessation) but did not reduce the number of growing season frosts resulting in an increase in frost damage. Within the ICHmc2, the lack of winter chilling became an increasingly important factor in 2080s climate scenarios. Lodgepole pine showed a small increase in its establishment ability over most of the CISR with the largest positive gains occurring in the ESSF ecosystems and SBSwk2 and SBSwk3 ecosystems. The key finding of this analysis is that lodgepole pine will likely exhibit a high degree of resistance to climate change across the majority of the CISR, even in the IDF portions.

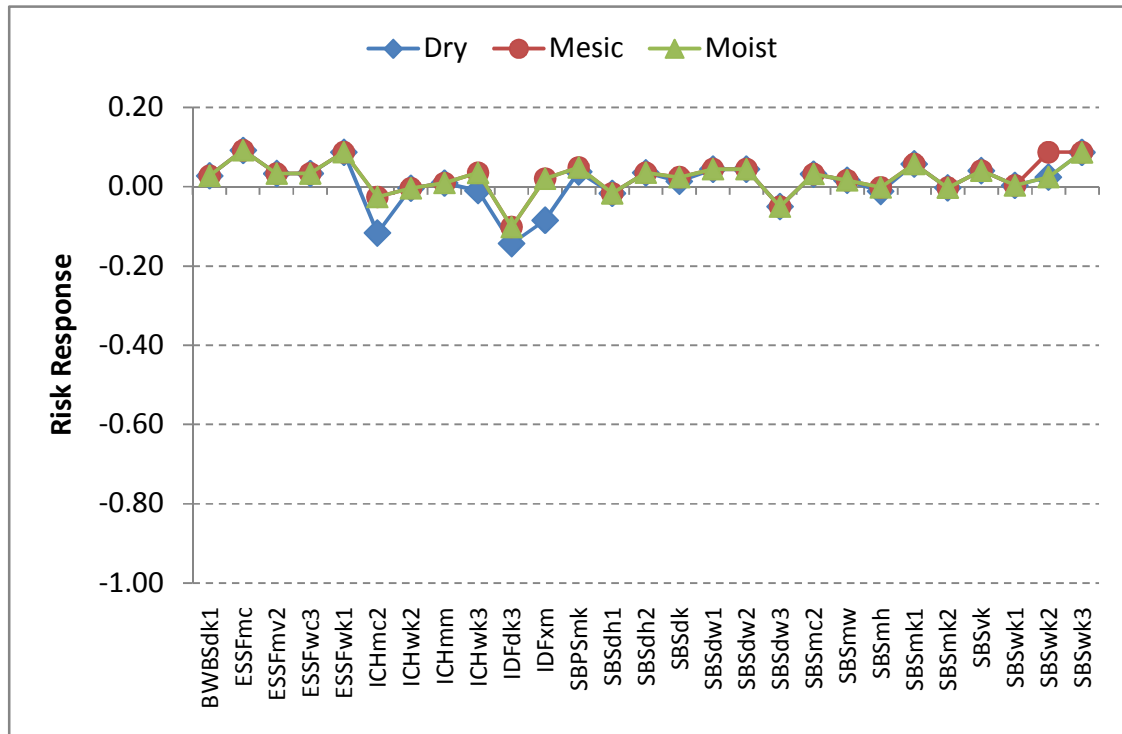


Fig 10: Risk response curve for lodgepole pine across central interior study area

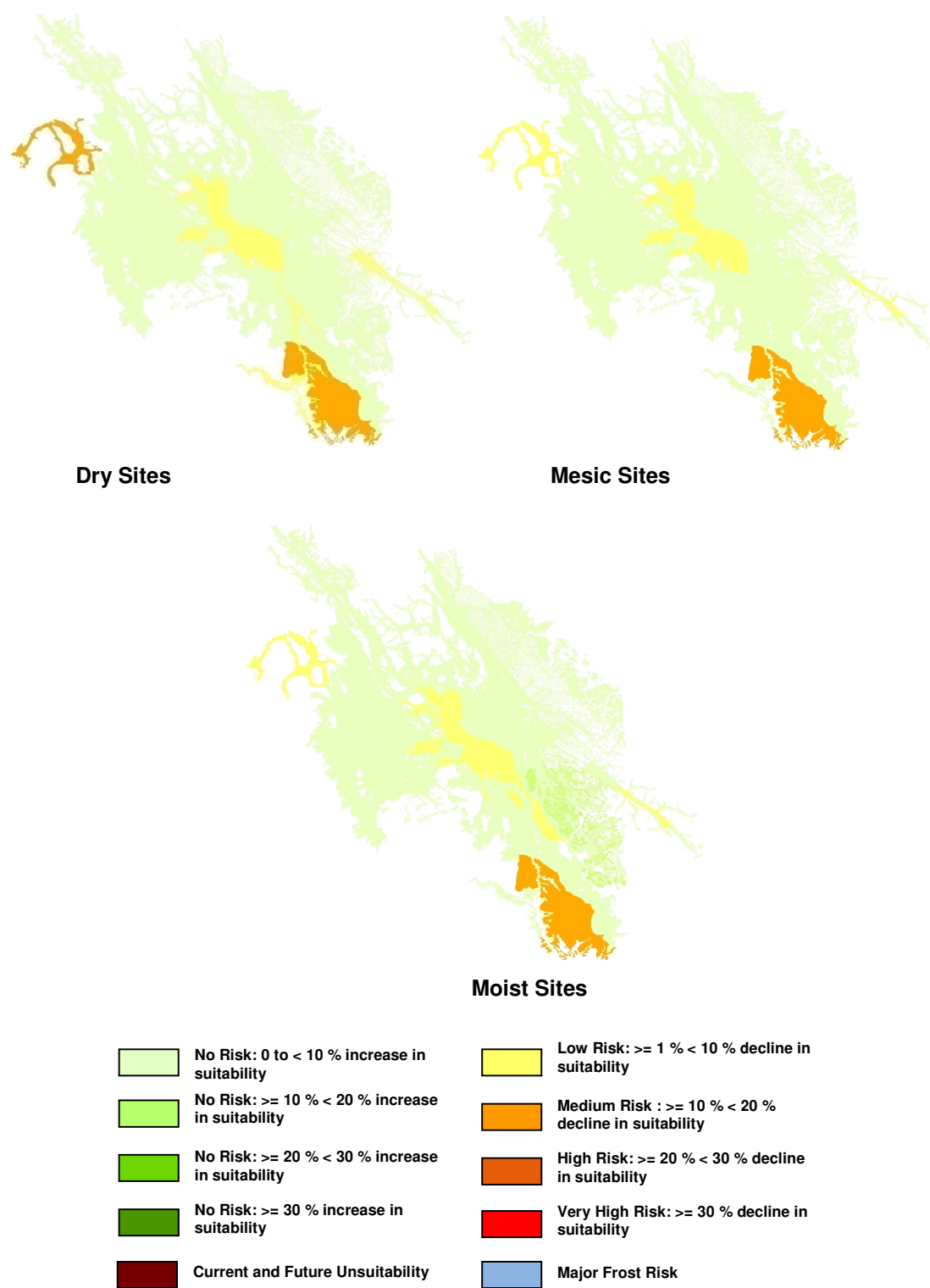


Fig 11: Risk maps for lodgepole pine for dry, mesic and moist sites across central interior study area

Across the IDF, SBPS, and warmer and drier SBS ecosystems, subalpine fir is largely absent, restricted to moist sites, and restricted to mesic/ moist sites respectively. As a result, the risk profiles in Fig 12 and 13 are restricted to the ecosystems and sites that the species commonly occurs in and on. Subalpine fir exhibited a high degree of risk to climate change; particularly on dry and mesic sites. On moist sites the species is at highest risk in the SBPS. On mesic sites, subalpine fir was found to exhibit a significant high risk in the SBSdh1 and SBSdh2 followed by a medium risk rating in the SBSdk, ICHmm, SBSmw, SBSmk1, SBSmk2, ICHmc2, ICHwk2, and ICHwk3 (see Fig 12 and 13). Like the two previous species and increase in suitability occurred in the ESSF ecosystems, particularly in the ESSFmc, and in the SBSwk2 and SBSwk3. On dry sites subalpine fir displayed high risk on all three sites. Significant risk was calculated for subalpine fir in the BWBSdk1, SBSmw, SBSmk1 and SBSmk2. The ICHwk2 was classified as a medium risk region while the ICMmc2, ICHmm, ICHwk3, SBSmc2, SBSvk and SBSwk1 were classified as low risk ecosystems due to a lack of winter chilling becoming an increasingly important factor in 2080s climate scenarios. Fig 13 illustrates the risk response of subalpine fir spatially; there are three prevalent trends that can be gleaned from risk analysis, they are: 1) the increase or maintenance of suitability within higher elevation ecosystems; 2) a decline in suitability on dry and mesic sites in the central region of the study area; and, 3) the role that edaphic variability plays in exacerbating and mediating this species risk to climate change. Subalpine fir's establishment coefficients under varying climate scenarios are provided in Appendix A.

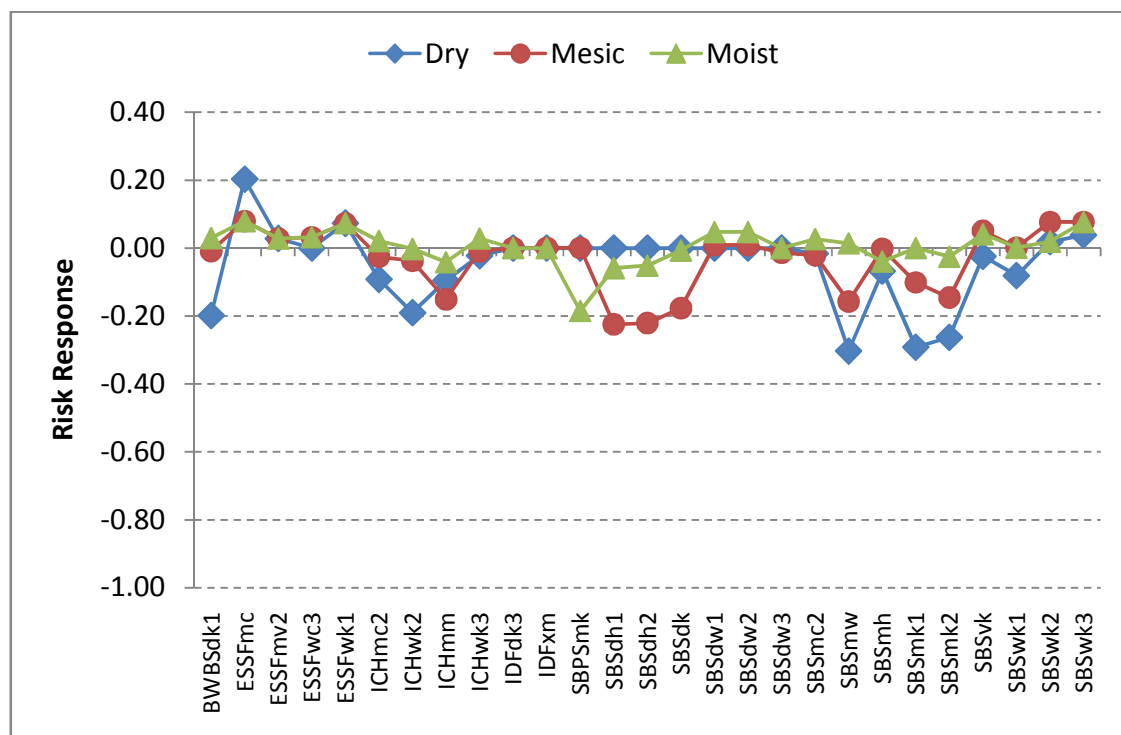


Fig 12: Risk response curve for subalpine fir across central interior study area

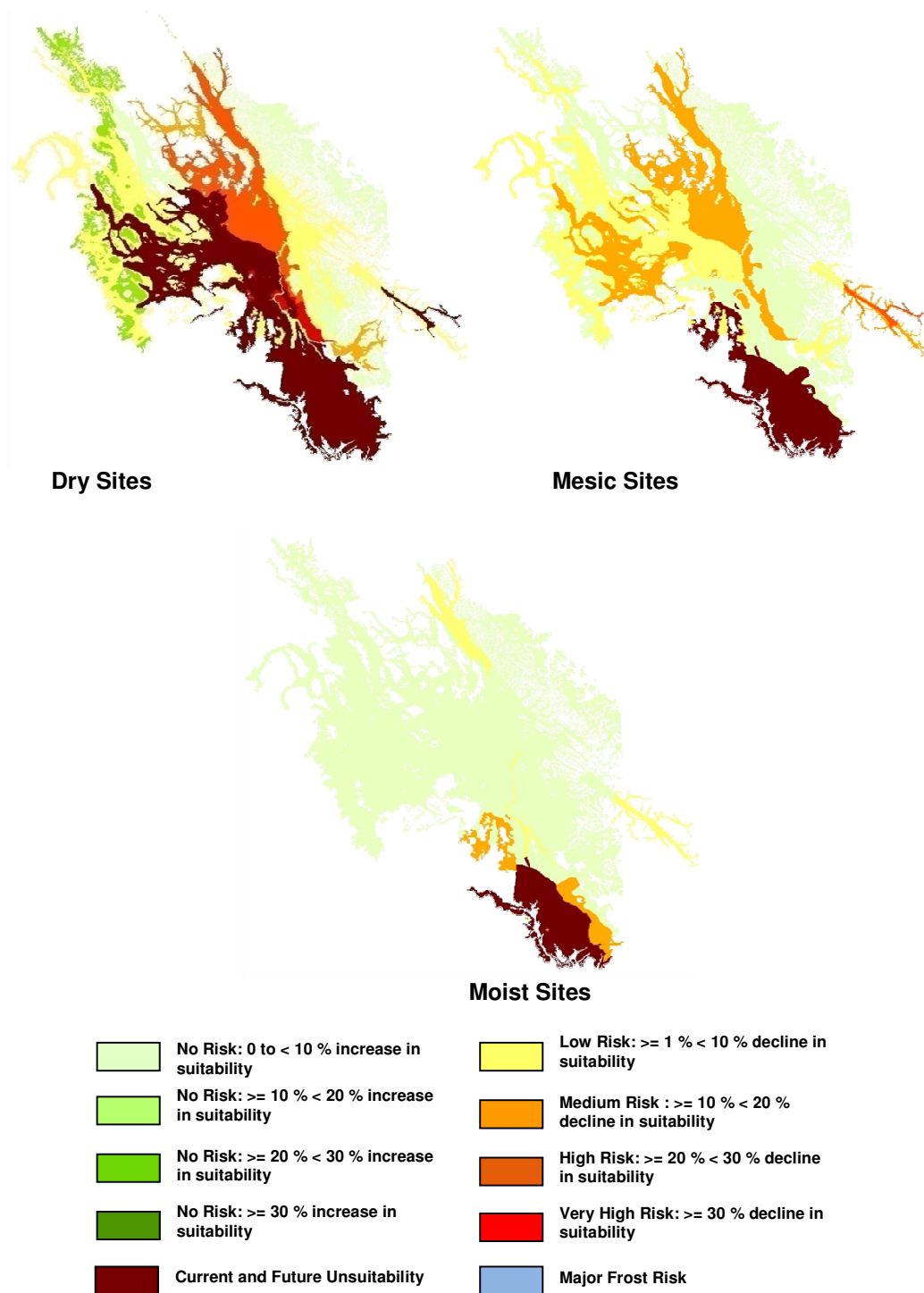


Fig 13: Risk maps for subalpine fir for dry, mesic and moist sites across central interior study area

The risk profile calculated for black spruce highlighted that the species ability to regenerate will most likely be unaffected by climate change on the sites that were considered in this analysis (Figs 14 and 15). Low risk ratings were calculated for mesic sites in the ICHmc2 and SBSdw3. Low risk was also categorised for both dry and mesic sites in the SBSmh and SBSmk1. Positive/ neutral responses (i.e. no risk) were calculated for the BWBSdk1, ESSFmv2, SBSdk (mesic sites only), SBSmc2 (mesic sites only) and SBSwk2 (all sites). Within the ICHmc2, the lack of winter chilling became an increasingly important factor in 2080s climate scenarios. Black spruce’s establishment coefficients under varying climate scenarios are provided in Appendix A (Figs A4a-c).

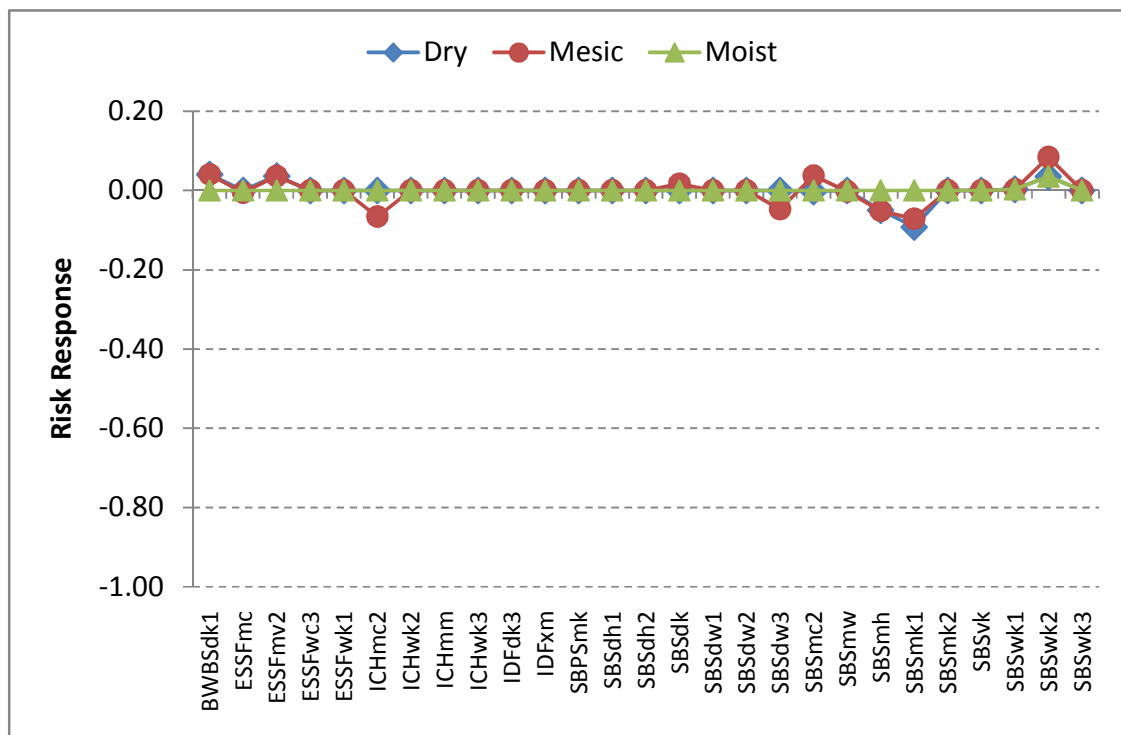


Fig 14: Risk response curve for black spruce across central interior study area

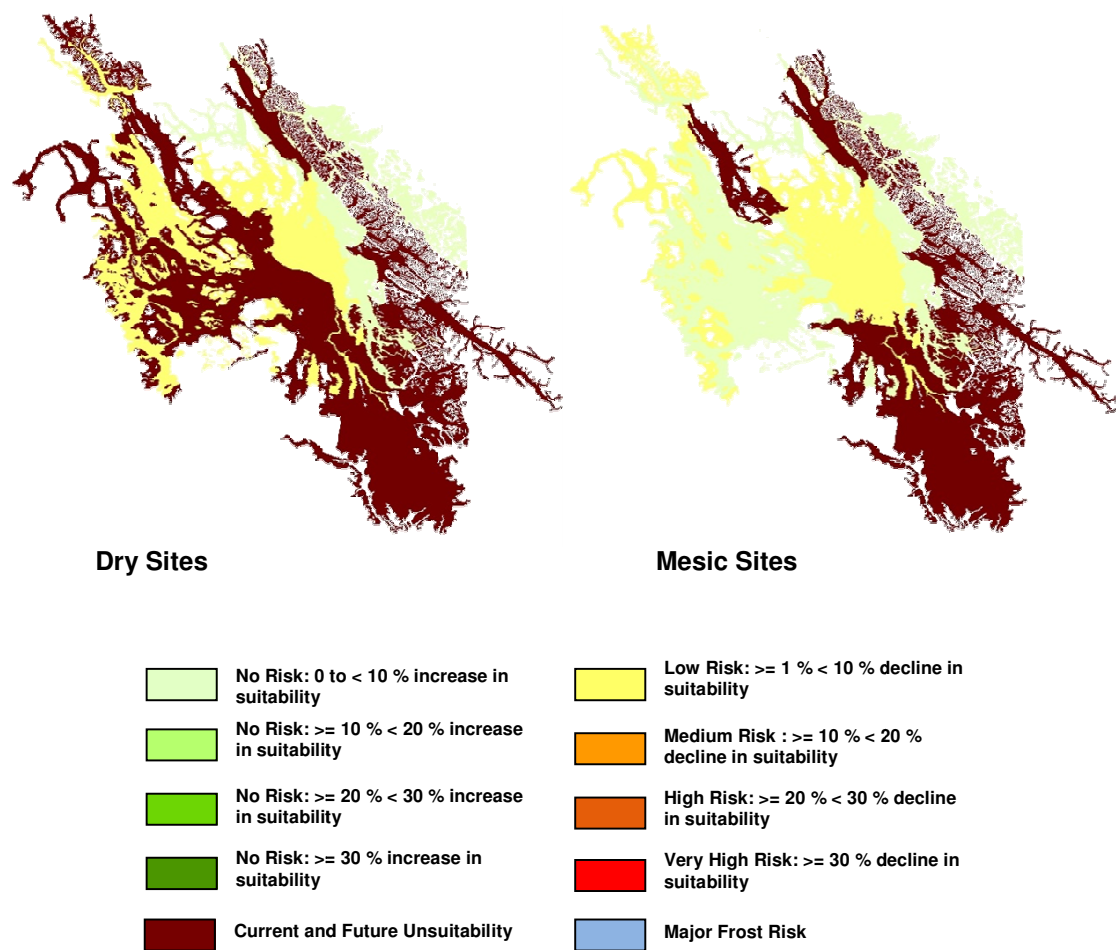


Fig 15: Risk maps for black spruce for dry and mesic sites across central interior study area

Engelmann spruce was found to exhibit the highest degree of risk to climate change in the CISR of all species (Figs 16 and 17). The risk response was calculated for the ESSF ecosystems only. In the ESSFmc and ESSFmv2 ecosystems a significant risk response was calculated across all site types. The risk response of Engelmann spruce on the dry site in the ESSFmc was lower than the mesic and moist sites which seem counter intuitive but the species was found to already be constrained by soil moisture on dry sites within this ecosystem (see Fig A5a-c in Appendix A). The risk calculated is relative to the degree of change from the baseline (i.e. historic results) which in this situation

highlights that the absolute decline in regeneration suitability may be greater on mesic and moist sites than dry sites within the ESSFmc but that significant risk exists on dry sites. Medium risk was calculated on all sites within the ESSFwc3 and ESSFwk1 ecosystems. Fig 17 illustrates the risk rating for Engelmann spruce across the CISR. The two factors that can be identified from Fig 17 are: 1) risk to Engelmann spruce occurs throughout the CISR; and, 2) significant high risk to climate change occurs in the leeward positioned ESSFmc and ESSFmv2 with the windward and wetter ESSFwk1 and ESSFwc2 mediating risk to a certain degree.

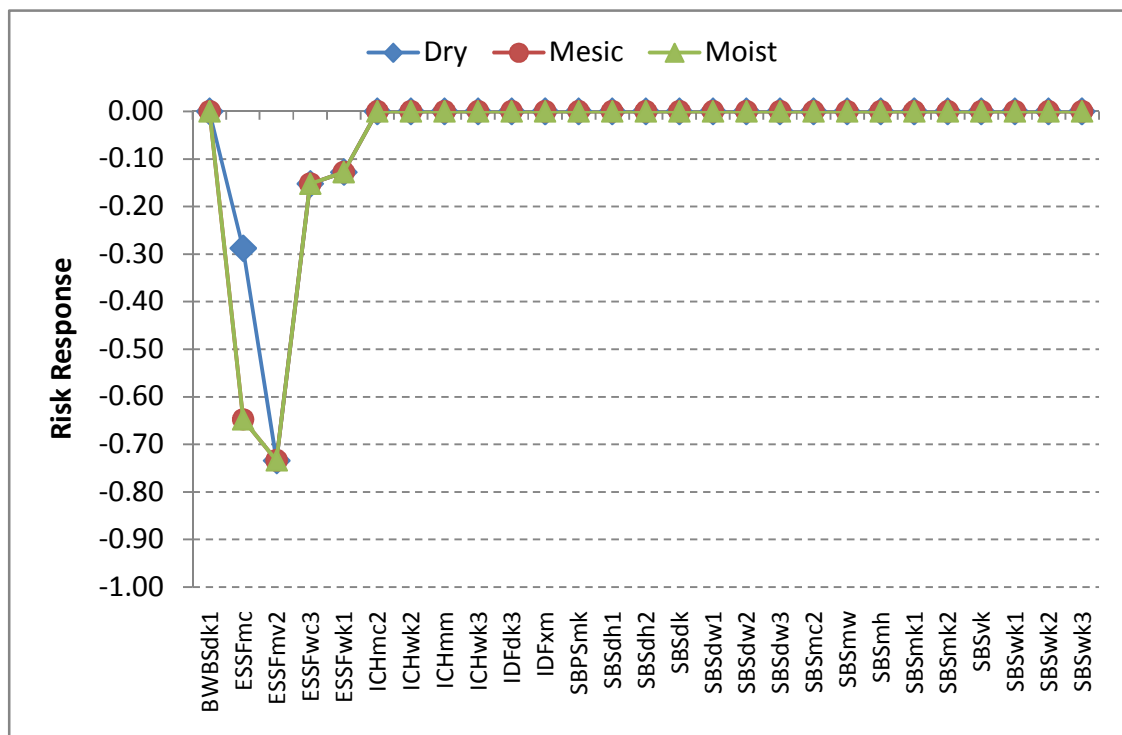


Fig 16: Risk response curve for Engelmann spruce across central interior study area

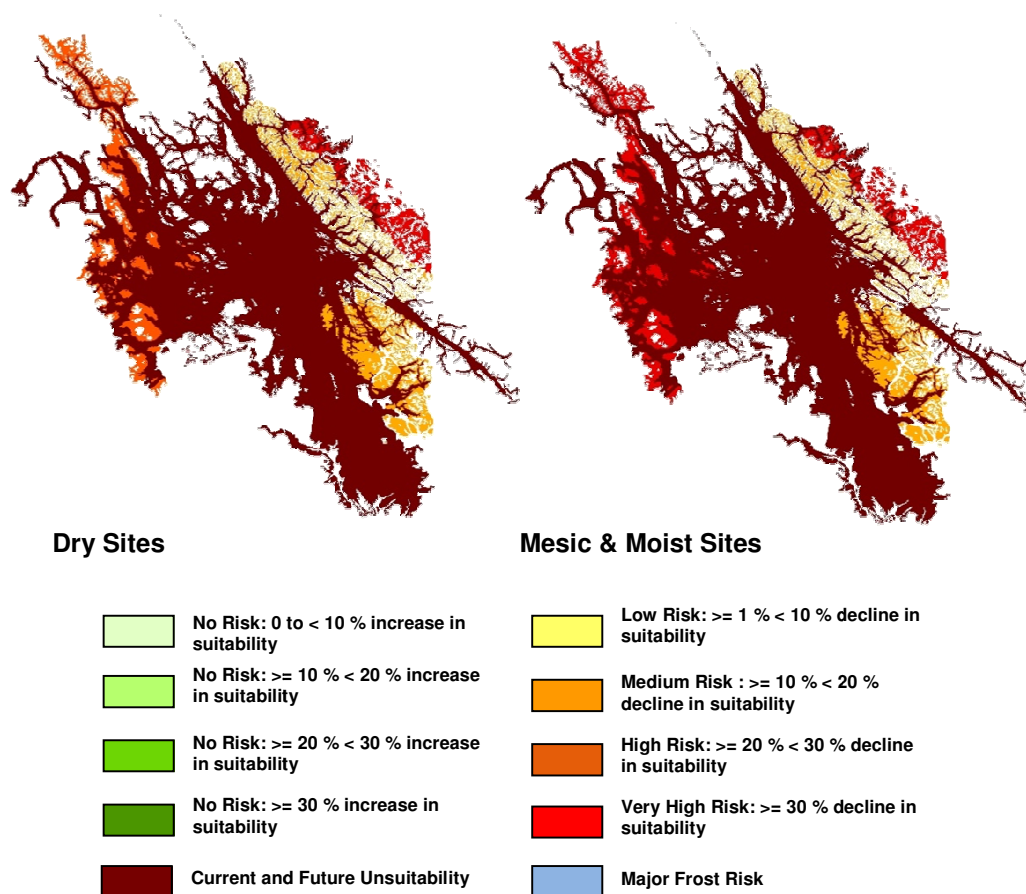


Fig 17: Risk maps for Engelmann spruce for dry, mesic and moist sites across central interior study area

Interior spruce's response curve (Fig. 18) illustrates and mixed risk response driven by edaphic variation between the site types. The highest risk response occurred for dry sites where significant risk ($P \leq 0.05$) was calculated in five of the ecosystems (IDFdk3, IDFxm, SBSdk, SBSdw3, SBSmw) and low to medium risk in 10 other ecosystems. The ESSF and wetter SBS ecosystems were the only areas that a neutral or small positive response was observed. On mesic sites the response of interior spruce was mediated with only one significant high risk rating (IDFdk3), one medium, and five low ratings. The moist site conditions further mediated interior spruces response with one medium risk response and six low risk ratings. Figure 19 spatially illustrates the divergent risk

responses between site types and the role edaphic variation may play in exacerbating and mediating species response to climate change. Interior spruce's establishment coefficients under varying climate scenarios are provided in Appendix A (Figs A6a-c). Similar to lodgepole pine, interior spruce received a low risk rating on mesic and moist sites in the SBSdw3 (see Figs 18 and 19) due to an increase in frost damage that occurred under the 2050s-1 scenario. Similar to subalpine fir, interior spruce exhibited an increase or maintenance of suitability within higher elevation ecosystems, a decline in suitability on dry sites in the central region of the study area, and highlights the need to consider edaphic variability in determining species responses to climate variability and change.

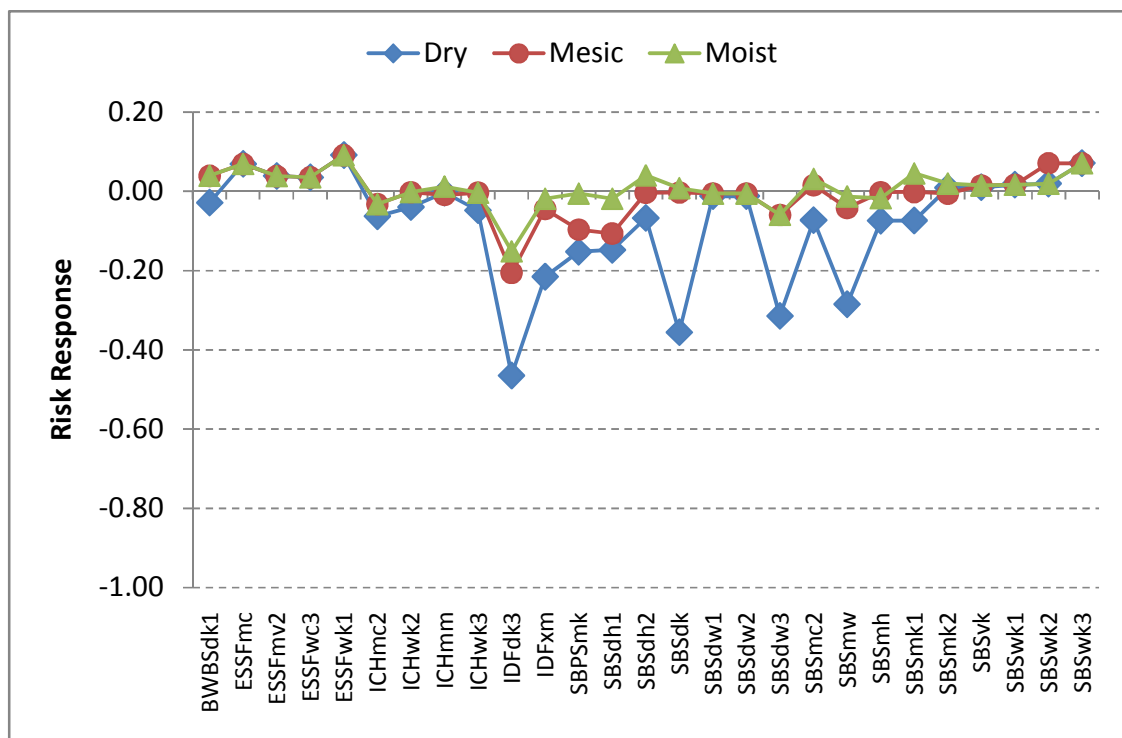


Fig 18: Risk response curve for interior spruce across central interior study area

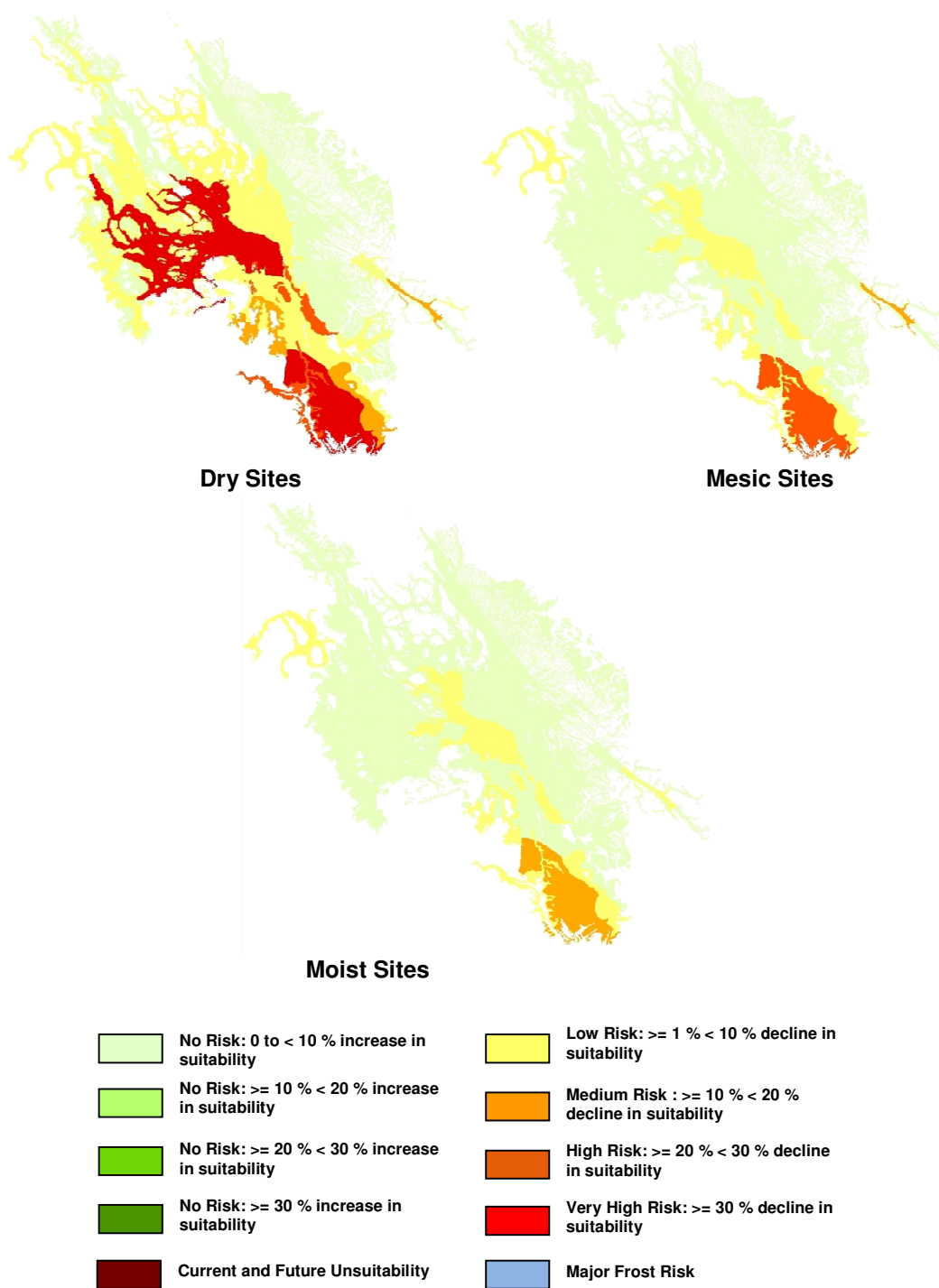


Fig 19: Risk maps for interior spruce for dry, mesic and moist sites across central interior study area.

Paper birch displayed variable responses and consequent risks to climate change within the CISR (Fig 20). On dry sites paper birch suffered declines in its establishment coefficients across the ecosystems that it occurs readily in (see Appendix A; Figs A7a-c) resulting in a low to high risk response in every ecosystem except the BWBSdk1, ESSF, SBSwk1, and SBSwk3. Within the ESSF ecosystems, paper birch responded favourably particularly in the ESSFmc and ESSFwk1 as growing season frost events declined (Appendix A, Figs A7a-c). The analysis highlighted that paper birch could already occur in the ESSF ecosystems covered in this study, although; according to the field guides to ecosystem and site series interpretation for the study region it only does so in the ESSFmc. Interestingly, only limited increases were modelled in the ESSFmv2 and ESSFwc3, an examination of the mechanisms that were affecting paper birch showed that growing season frosts were likely to be more of an issue in these ecosystems versus the ESSFmc and Esskwk1 in the future. Paper birch also showed an increase in suitability within the SBSwk2, wk3, mk1, mk2, and dh2 ecosystems. Across all sites within the ICH ecosystems paper birch exhibited some degree of risk with significant risk occurring in the ICHmc2 as the lack of winter chilling becoming an increasingly important factor in 2080s climate scenarios. Significant high risk was identified for both mesic and moist sites within the IDF ecosystems while medium risk was classified for the SBSmw and SBSmh ecosystems. The SBSvk was rated as an ecosystem where paper birch could be considered to be at low risk to climate change but will likely retain a high establishment coefficient, particularly on mesic sites(see Appendix A; Fig A7b). Figure 21 represents the risk of paper birch to climate change spatially. Paper birch responded equally on mesic and moist sites with dry sites exacerbating the species response to climate change.

Like the majority of the CISR's species, the higher elevations become more suitable on all sites for paper birch; the southern warmer and drier ecosystems will likely become areas of high risk as growing season water deficits limit the species ability to establish. The northeast portion of the CISR becomes the region that edaphic variability may play a larger role in mediating this species response with neutral and positive responses occurring on mesic and moist sites but negative responses on dry sites (see Fig 21).

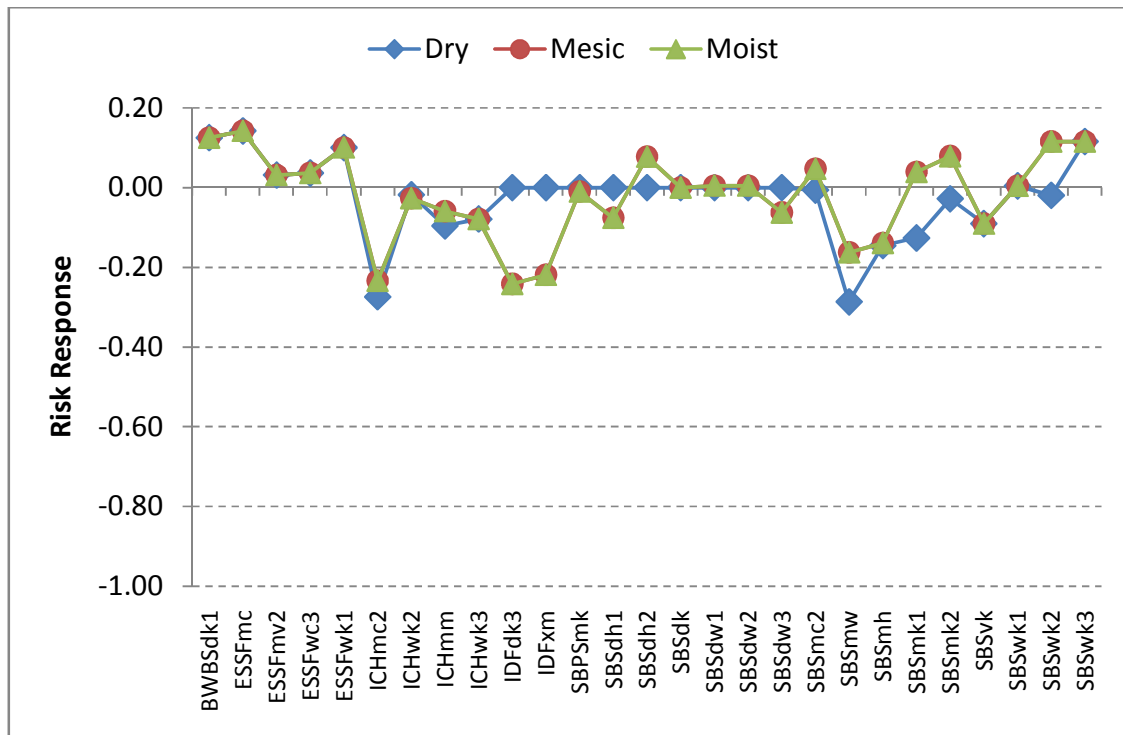


Fig 20: Risk response curve for paper birch across central interior study area

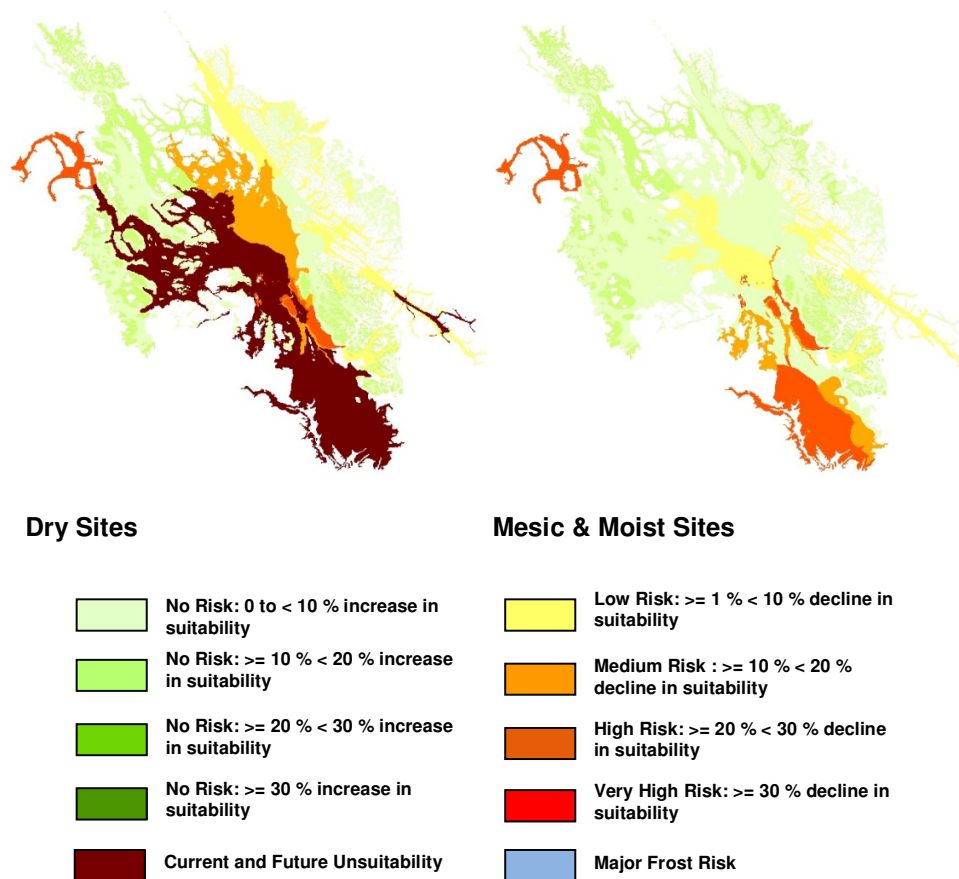


Fig 21: Risk maps for paper birch for dry, mesic and moist sites across central interior study area

Trembling aspen, like lodgepole pine showed a relatively static response to climate change across the CISR (Figs 22 and 23). The highest risk scores occur for the IDF ecosystems where increasing soil moisture deficits have a limited impact on aspen, particularly on dry sites. Trembling aspen displayed positive responses across the remaining ecosystems and site types except in the ICHmc2, ICHwk2 and SBSmw where small declines in suitability were modelled but establishment coefficients remained very high (Appendix A, Figs A8a-c). A decline in winter chilling was the limiting factor in 2080s climate scenarios within the ICHmc2 and wk2 ecosystems. Figure 23 illustrates the risk maps for trembling aspen across the CISR ecosystems. The risk maps show how

resilient trembling aspen is across the region to climate and how edaphic variability will play a minor role exacerbating or mediating the species response to climate change except in the warmer, drier portion of the region.

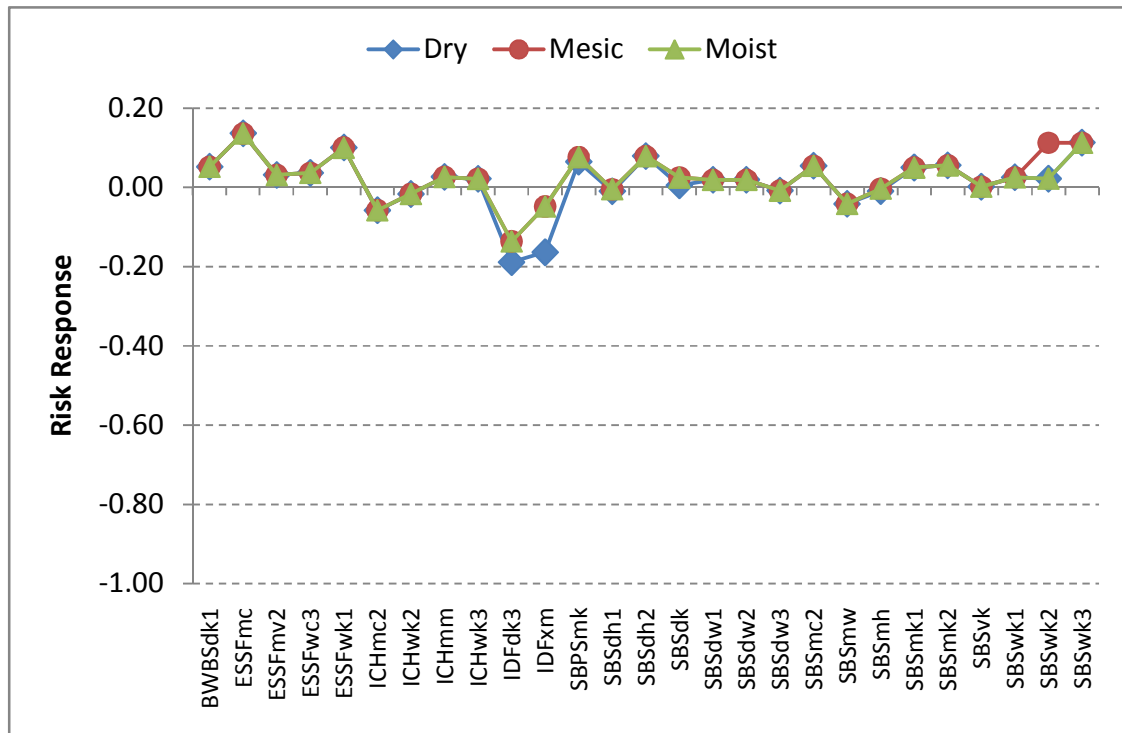


Fig 22: Risk response curve for trembling aspen across central interior study area

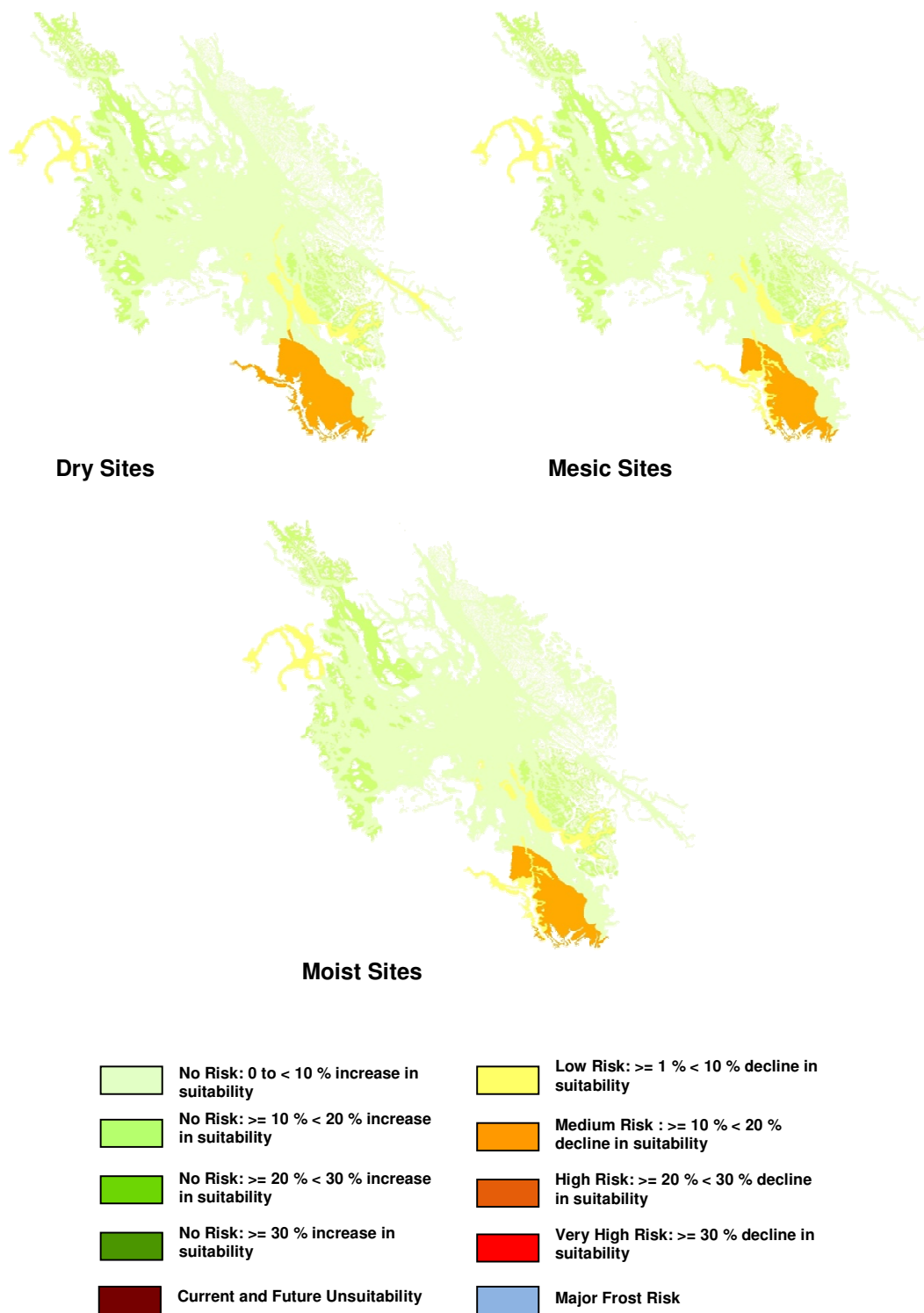


Fig 23: Risk maps for trembling aspen for dry, mesic and moist sites across central interior study area.

Douglas-fir was the CISR species that benefited the most from climate change in this analysis. As highlighted in Figures 24 and 25, Douglas-fir showed positive increases in its establishment coefficients in 24 out of 27 of the ecosystems while it incurred a small loss in suitability across the remaining three ecosystems. As can be seen in Figures 24 and 25 Douglas-fir responded equally across all sites which highlights that edaphic variability may have little effect in mediating or exacerbating this species response across the CISR in the future. Douglas-fir was classified at low risk in the ICHmc2; however, it is currently not found within this ecosystem though the modelling suggested that it has a fairly high establishment coefficient under current climate conditions (0.78). See Appendix A, Figs A9a-c, for the establishment coefficients of Douglas-fir across the CISR. Douglas-fir was modelled to have significant increases in suitability in the ICHwk2, IDFd3, IDFx, SBPSmk, SBSdh2, SBSdk, SBSmc2, SBSmw, SBSmk1, SBSmk2, SBSwk1, SBSwk2, and SBSwk3. The increase in suitability across the study area resulted from decline in growing season frosts, particularly in the SBPSmk, although in some cases the severity of the frost season did not change to a large degree as the growing season initiated earlier in the spring and lasted longer in the autumn when frost occurrence remained high. The SBSdw2 received a risk rating of low despite an average increase in suitability under climate change (see Appendix A, Figs A9a-c) as frost was a constraining factor in the 2050s-1 climate scenario. The spatial risk map for Douglas-fir (Fig 25) highlights an important factor that will likely constrain the ability of Douglas-fir to establish in the ESSF ecosystems of the study area. The modelling showed that under the historic climate Douglas-fir had establishment coefficients of 0.29 in the ESSFwk1, 0.3 in the ESSFmc, 0.55 in the ESSFmv2, and 0.66 for ESSFwc3. These high coefficients

would suggest that Douglas-fir could establish readily in latter ESSF ecosystems; however, an investigation of the mechanisms that were affecting the species identified that in 30% of the climate scenarios a lethal frost event occurred. The occurrence of a killing frost event every three to four years coupled with annual growing season frosts are major constraints on survival and growth that needs to be considered for this species. Under the climate change scenarios the occurrence of killing frosts declined but the occurrence of such events ranged from five to 10 % of the time under the range of climate change utilised in the study. For this reason, these ESSF ecosystems were classified as having a “Major Frost Risk”. The other interesting process that was identified in the investigation of Douglas-fir’s high suitability scores was that the growing season was initiated on average in August within the ESSF. In comparison, subalpine fir was found to initiate growth at the end of May. Under climate change, bud flush in subalpine fir moved towards the middle of May while Douglas-fir moved to the beginning of July; a difference of six weeks. These processes highlight the affects that frost and colder temperatures will have on the ability of Douglas-fir to establish in these higher elevation ecosystems and also highlight the need to consider the affects of climate on growth in interaction with competition for resources with other species.

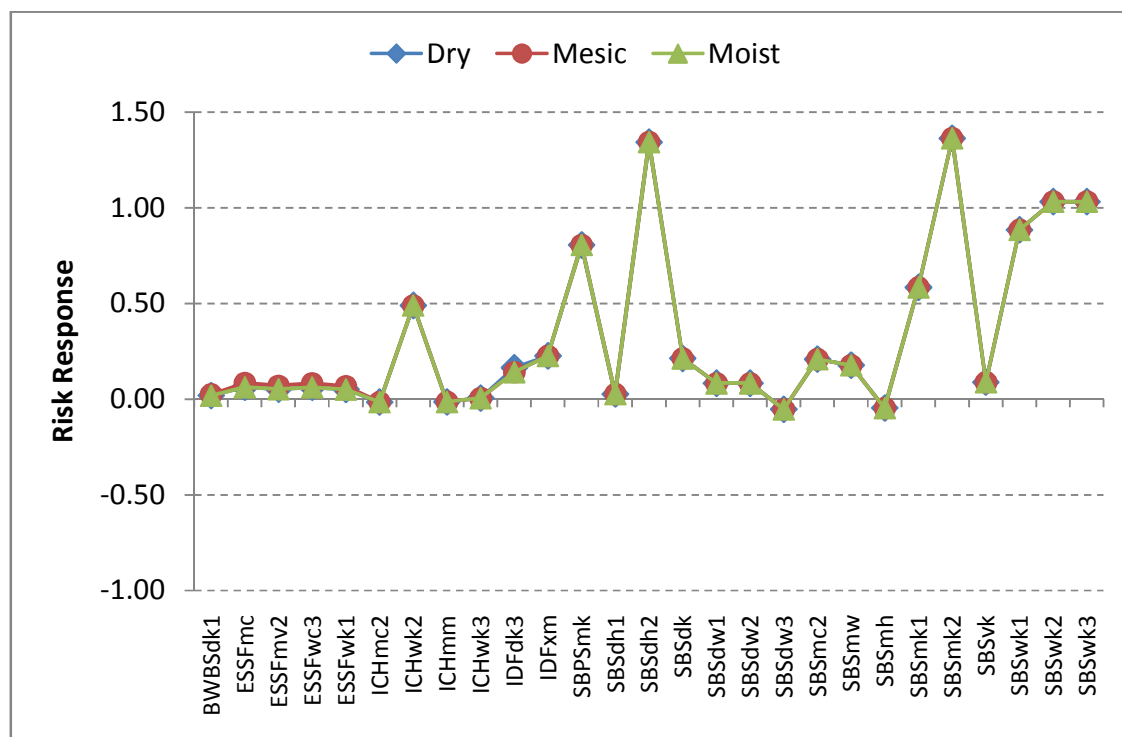


Fig 24: Risk response curve for Douglas-fir across central interior study area

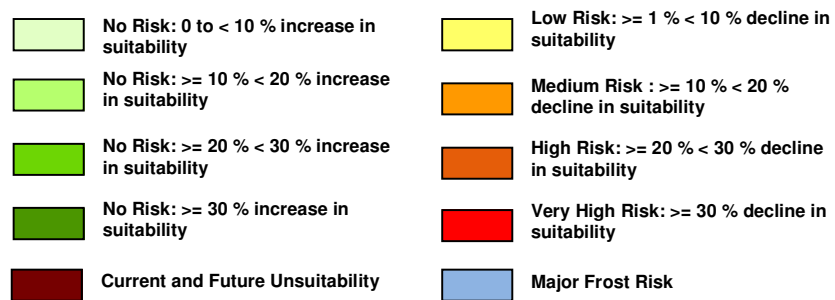
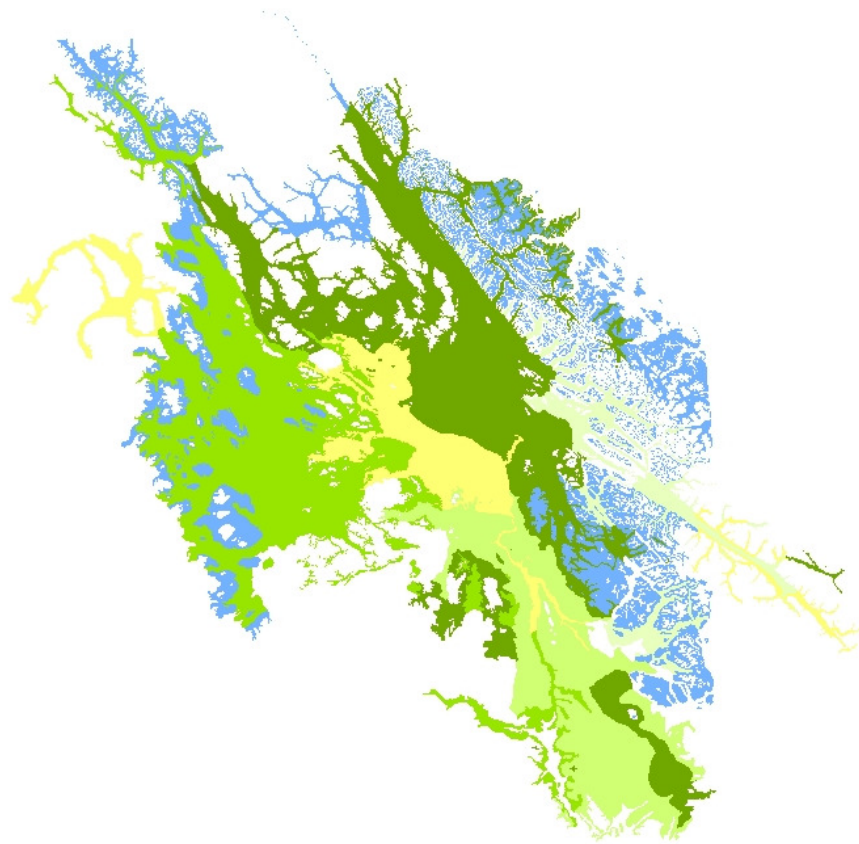


Fig 25: Risk map for Douglas-fir for dry, mesic and moist sites across central interior study area. Same risk response on all sites.

Discussion

Responses and Processes

Predicted climate change in North America will be comparable or greater than what occurred 14,000 to 9,000 years ago during the transition from the late Pleistocene glacial periods to the Holocene (Bartlein *et al.*, 1997). During this period of climatic change, variations in seasonal distribution of insolation, temperature and precipitation led to the dismantling of glacial communities and created a series of rapidly changing biotic associations. Plants adjusted their ranges independently to meet their individual climatic requirements and rates of response varied as a function of species ability to disperse and colonise (Bartlein *et al.*, 1997). Hamann & Wang (2006) predicted that the ecosystems of British Columbia would shift to higher elevations and latitudes in response to climate change and that the ecosystem compositions would more or less remain static. Cumming and Burton (1996) predicted that the forest ecosystems in British Columbia may shift upward in elevation, with some species disappearing from some of the ecosystems. This implies broad climatic zones of ecosystems may shift but that the species composition of these zones may also change as species respond individualistically. Based on paleoecological and modelling studies it is generally expected that species will respond individualistically to climate change (Bartlein *et al.*, 1997; Hansen *et al.*, 2001; Iverson & Prasad, 2001; Shafer *et al.*, 2001). In this study, species did respond individualistically as their establishment coefficients shifted independently of one another over time and space. Species showed uniform responses in their increases in suitability the ESSF and SBSwk ecosystems with the exception of Engelmann spruce. It has been commonly

hypothesised that the forest ecosystems of western North America will shift upwards in elevation in response to climate change (Aber *et al.*, 2001). In particular, ecosystems that are water-limited are expected to shift upwards or downwards depending on the change in water balance. Drought has been found to facilitate rapid changes in ecosystem composition (Allen & Breshears, 1998). In this study, the current CISR species were found to consistently respond to increases in growing season water deficits in the warmer and drier ecosystems, particularly on site type 1 (dry); however, in the cool/ cold and moist/wet ecosystems greater differentiation between species and site types was modelled.

The lack of winter chilling and growing season frosts are also considered potential driving factors that drive species distribution and can facilitate change (Burton & Cumming, 1995). In this study, declines in chilling were negligible in the ESSF, SBS and IDF but was very important factor in the ICH ecosystems; particularly the ICHmc2 where the majority of species exhibited a decline in suitability due to a decline in winter chilling. Frost days were modelled to decline under predicted climate change along with frost damage; however, it is important to acknowledge that frost events will still occur during the growing season as bud burst occurs early in the season cessation of growth occurs later in the autumn. The growing season was modelled to initiate 2 to 14 days earlier in the ESSF, 17-32 days across the SBS, 13-28 days across the IDF and 30 to 46 days earlier across the ICH ecosystems from 1.7 °C increase in temperature and onwards. With a 1 °C increase in temperature or less the growing season did not increase substantially as many of the climate scenarios were still within the range of observed

variation. Increases in temperatures can restrict and prevent species from re-establishing on a site (Franklin *et al.*, 1992). The increase in growing season intensity, as measured by growing degree days, became an important mechanism impacting Engelmann spruce as climate changed. A 1.5 °C increase or greater appeared to be a tipping point for this species in terms of its response to this mechanism.

The risk species may face to climate will also be ameliorated by local microclimatic and edaphic conditions (Nitschke & Innes, 2006). For example, riparian areas have been found to provide areas where species can persist under large changes in climate (Aide & Rivera 1998; Burke, 2002). Ashton (1976) found that species had divergent responses between sheltered and exposed sites to a severe and prolonged drought. In this study, we found species responded with increased sensitivity on sites where drought stress may be exacerbated by shallow - coarser textured soils. The soil type upon which all species responded exhibited fairly neutral responses to changes in soil moisture caused by increases in evaporative demand were the moist sites. Some species remained resistant to these changes on mesic sites as well across the CISR whereas other species (subalpine fir and interior spruce, for example) showed divergent responses on mesic sites between ecosystems. These findings suggest that sites with moist to wet edaphic conditions may be important for maintaining species and ecosystems across the CISR under climatic change while the drier sites and regions will see the greatest changes. The modelled species response supports the conclusions of Aide & Rivera (1998) and Burke (2002) on the importance of sites with wetter and cooler climatic and edaphic conditions in maintaining species over time within a landscape matrix of warmer and drier conditions.

These areas can be regarded as bastions of biodiversity as they may serve as areas that maintain communities as climatic refugia (Kirkpatrick & Fowler, 1998; Theurillat & Guisan, 2001; Burke 2002; Rouget *et al.*, 2003). They can also be regarded as areas of robustness where actions can be made based on an understanding of ecosystem function under uncertain futures. Actions in these areas will likely be robust to uncertainty and reversible if actions are misguided (Carpenter *et al.*, 2001). Maintenance of species inertia within these areas is very important since it will assist the ability of the species to cope with rapid environmental change (Brereton *et al.*, 1995).

Comparison with Hamann & Wang (2006)

Based on species-specific responses modelled in this study, it appears that there are some congruencies with the findings of Hamann & Wang (2006) but there are also some differences. Hamann & Wang (2006, Appendix C) predicted that the frequency of black cottonwood (described as *Populus balsamifera*) in the ICHmc2 and ICHmm may be maintained, may decline in the SBSdk, and may increase in the remainder of the CISR. In this study the risk analysis suggests that the ICHmc2 and ICHmm will decline in suitability while suitability will be maintained in the SBSdk. Negative responses were also modelled for the ICHmm and IDFx_m which diverges from the estimates of Hamann & Wang (2006). The ICH divergence is due to the effects of chilling while the IDF is due to drought stress which was driven by soil characteristics that are not considered in the approach used by and Wang (2006). In comparison with Hamann & Wang (2006, Appendix D), the risk response map for lodgepole pine shows a marked similarity in the ecosystems that this study identified at risk (IDF, ICH and SBSdw3). They predicted a

decline in lodgepole pine frequency in these areas. Similarities also exist in the modelled increases in the suitability of the higher elevation ecosystems. The main divergence in the two studies is the predicted decline in frequency for lodgepole pine across the central portions of the CISR by Hamann & Wang and the maintenance of its establishment ability in this study. For subalpine fir, Hamann & Wang (2006, Appendix C) predicted a decline in frequency across the entire CISR with the exception of the ESSF ecosystems. In this study, subalpine fir was modelled to exhibit a decline in establishment suitability across the CISR on dry and mesic sites while on moist sites it remained resistant to predicted change. For interior spruce (described as *Picea glauca*) the differences were even more polarised with this species maintaining suitability in the ESSF zones of the CISR and on mesic to moist sites across the majority of the ecosystems. With the exception of this species response in the ESSF and wetter SBS ecosystems comparable declines in suitability predicted by Hamann & Wang were only found to occur on dry site types. These findings highlight the role that edaphic variation may play in mediating species responses which are not accounted for in approach of Hamann & Wang. In comparison, the response of paper birch between both studies is mixed when you consider edaphic variation. On dry sites this species was modelled to suffer declines in establishment suitability across much of the CISR which is in contradiction to the findings of Hamann & Wang. Convergence in findings for mesic and moist sites appears strong for each ecosystem except the IDF and SBPS ecosystems at the southern portion of the CISR. The results for Douglas-fir compare favourably between the two studies with increases predicted throughout the region. The findings of both studies suggest that Douglas-fir could become a more frequent species as its ability to regenerate and establish increases

across the CISR under climate change. A degree of caution should be exercised in some ecosystems with Douglas-fir due to the persistence of growing season frosts which may restrict this species to warm southerly aspects and sites not affected by cold air drainage and pooling (i.e frost hollows). The two studies utilised different methods: correlative versus process-based and non-edaphic versus edaphic and also different climate change scenarios. Correlative climate envelope approaches use different variables and do not account for non-linearities which can lead to divergent responses when compared to more process-based approaches (Ibanez *et al.*, 2007). Hamann & Wang also focused on the ecological niche while this study focussed on the regeneration niche so there are many possible factors that could cause the differences in potential species responses to climate change. From a risk assessment point of view the similarities highlight important regions where regeneration and ecological niches appear to be harmonised and thus climate change impacts may be felt more broadly whereas in areas of divergence a species may be at greater risk within the regeneration niche than within the ecological niche which is dominated by species within their mature/ adult stage. Grubb (1977) described the regeneration niche as being narrower than the niche space occupied by adults and this may be reflected in this analysis. Further divergence appears to be driven by the consideration of edaphic variation in this study. Heterogeneity in edaphic conditions can result in a differentiation in species response, enabling some species potentially to cope with change at the local-scale but not the regional-scale (Theurillat & Guisan, 2001).

Species Resistance and Ecosystem Resilience

Measuring the response of species and ecosystems to the uncertainty of climate change, through the concepts of ecological resilience and resistance is one method for understanding future response and risk (Hansell & Bass, 1998; Turner *et al.*, 2003). With exception of the IDF ecosystems the majority of species provided some degree of resistance to climate change, this however was dependant on site type. In a majority of these ecosystems lodgepole pine, and trembling aspen exhibited high resistance across all site types. Interior spruce, black spruce and paper birch demonstrated high resistance on mesic to moist sites while subalpine fir and black cottonwood showed high resistance on moist sites. For the species that show variation in responses due to edaphic variation a slow decline in frequency may occur over time on dry to mesic sites, but not on moist sites, as regeneration success declines. Douglas-fir showed high resistance and will likely benefit the most from climate change; though in higher elevation and frost prone areas, lodgepole pine on dry to mesic sites and interior spruce of mesic to moist sites will likely remain or become the most frequent species during the establishment phase. Within the ESSF zone the greatest changes in species frequency may occur with Engelmann spruce modelled to suffer significant declines across all site types, subalpine fir remaining resistance across all site types, and suitability increasing for most other species. It is plausible that within the ESSF ecosystems of the CISR, particularly the leeward located ecosystems, the regeneration practices currently applied in the current SBS ecosystems of the CISR may be more relevant in the future. The results highlight that the resilience of these ESSF ecosystems may be compromised in the future if Engelmann spruce cannot sustain its ability to regenerate. The IDF, ICH and BWBS

should remain resilient since they should retain their dominant species though changes in composition and frequency may occur as regeneration potential increases and decreases for species. Within the SBS ecosystems, a mixed degree of resilience is likely to exist with the wetter and cooler systems being highly resilient and the drier and warmer regions exhibiting less resilience. The regeneration practices currently applied in the Montane Spruce ecosystems of southern BC may be more relevant in the future within certain SBS ecosystems of the CISR.

Key to undertaking management actions is the knowledge of species risk and vulnerability from which informed and planned decisions can be made. Vulnerability measures the response of a species and can be used to define the risk of a species and an ecosystem. A species-level approach that examines the establishment ability of a species can provide a means to measure the resilience and resistance of a species to any stressor. The more resistant a species is the less vulnerable that organism is to a stressor in a specific time and place and the lower the consequent risk. The collective response of the species in a community can be used to determine ecosystem vulnerability and risk. As a stressor increases in magnitude, a breaking point may be reached. This point will vary between species and may cause the eventual disassociation of the current system and the creation of a new system. In this study, species were found to respond to climate change in different directions and at different degrees of climate change. The climatic thresholds that caused changes in the establishment coefficients ranged from 1.3 to 3.7 °C. This variability resulted from the interaction between species ecophysiology, climate, topographic and edaphic conditions. The variation illustrates the complexity of species

and ecosystem response but also highlight the potential resilience that is built into to ecosystems at the landscape-level.

Managing Species and Ecosystems under Climate Change

Management plans and policies that incorporate the current and future spatial arrangement of species are required to conserve species under environmental change (Barrio *et al.*, 2006). The achievement of sustainable management within the region will require the fostering of species and ecosystem resilience within the region. This can only be achieved by integrating an understanding of species vulnerabilities and response thresholds into management actions that serve to mediate species response and foster resilience to the stressor of climatic change. The fundamental decision that needs to be made is whether to protect the current mix of species or manage areas simply for the maintenance of diversity. Management actions that would enable a species to move through environmental gradients may provide viable means for protecting specific groups of species, while actions that seek to maintain species within heterogeneous sites may or may not; instead, they may facilitate a change in species composition (Halpin, 1997). The individualistic response of species suggests the need to manage at the species-level rather than the ecosystem-level (Bush, 2002). Management actions that are made based on the climatic optima of species are recommended by Peters (1992) as a means of achieving this, so long as the management actions are flexible. This flexibility can be achieved by using an adaptive approach where understanding from models is used to identify potential species which are then tested in provenance trials or incorporated at incremental stages into our reforestation policies as our understanding of species and ecosystem response becomes knowledge.

Conclusion

Species have always responded to climate change by shifting around regions and landscapes over time. Predicted future climate change will be occurring at a much greater rate than historically observed and this means that species and ecosystems will be placed under intense pressure to either adapt or move. The magnitude of predicted climate change in the CISR resulted in species-specific affects on the establishment ability of the dominant species within the study region. In some cases, a species' response was found to be exacerbated or mediated by edaphic conditions. Overall a diverse range of responses were modelled which resulted in a mixture of risks to climate change being calculated at the species level. Results were mixed in comparison with previous estimates of species response to climate change for the region with some species modelled to incur less negative responses and others more negative. The results of this study suggest that forest managers may be able to manage many of the ecosystems and site series within the CISR as currently done, even under a high degree of climate change; while other sites will require novel approaches to ensure species and ecosystem health and vitality. This study only focussed on the regeneration niche; however, to understand how climate change will truly affect species, we need to include the affects of inter-species competition and disturbance. Further research is needed to incorporate these important processes in order to bridge the gap between the regeneration and ecological niches of a species.

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Appendix A:

Species response to varying degrees
of climate change across central
interior study area

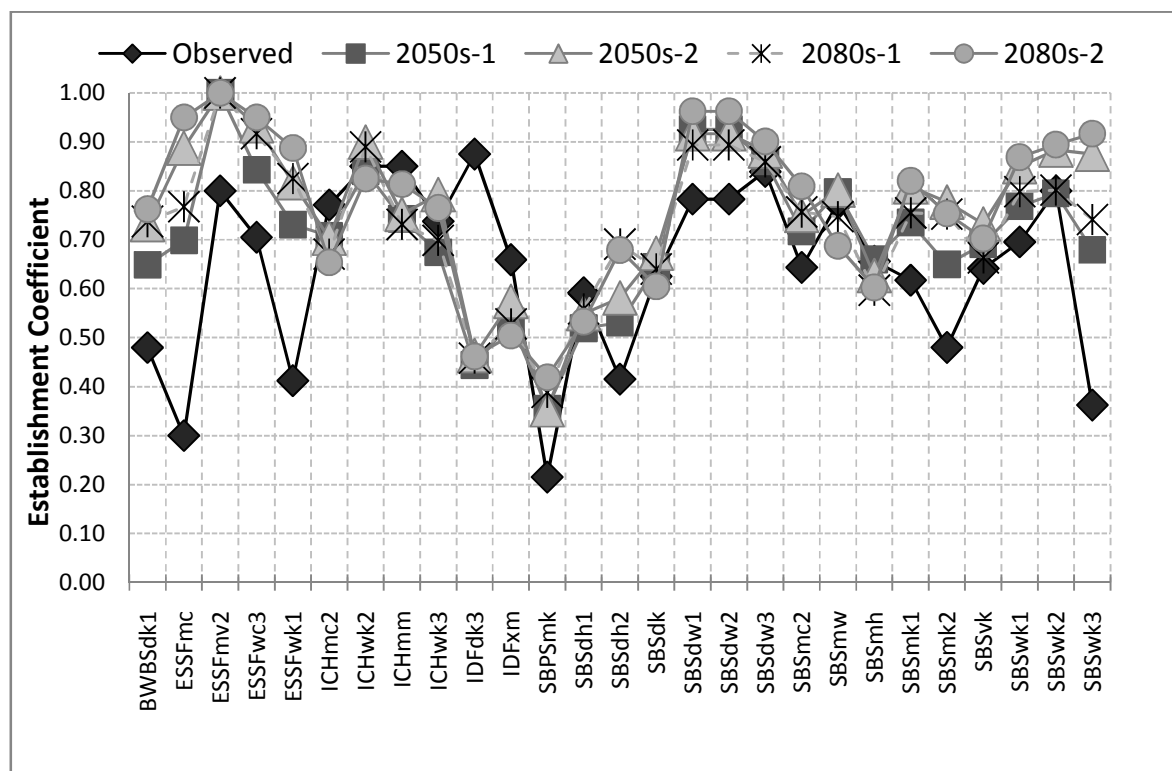


Figure A1a: black cottonwood response to varying degrees of predicted climate change on moist sites

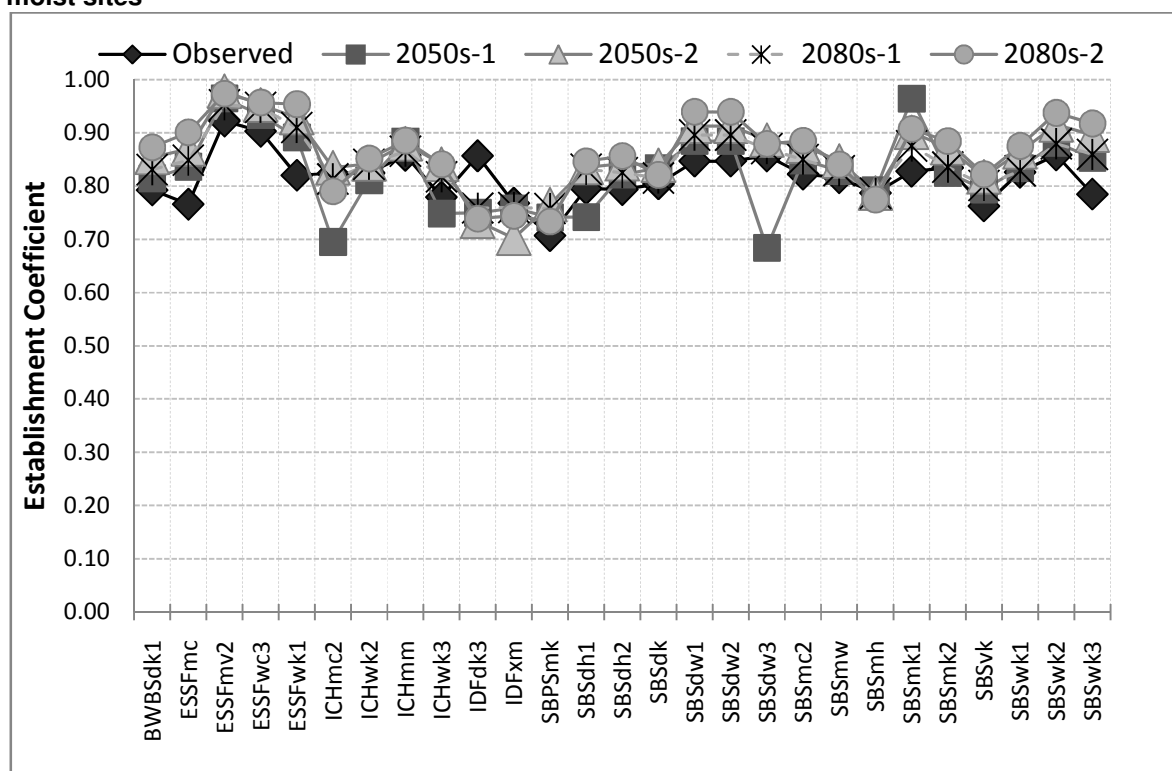


Figure A2a: lodgepole pine response to varying degrees of predicted climate change on dry sites

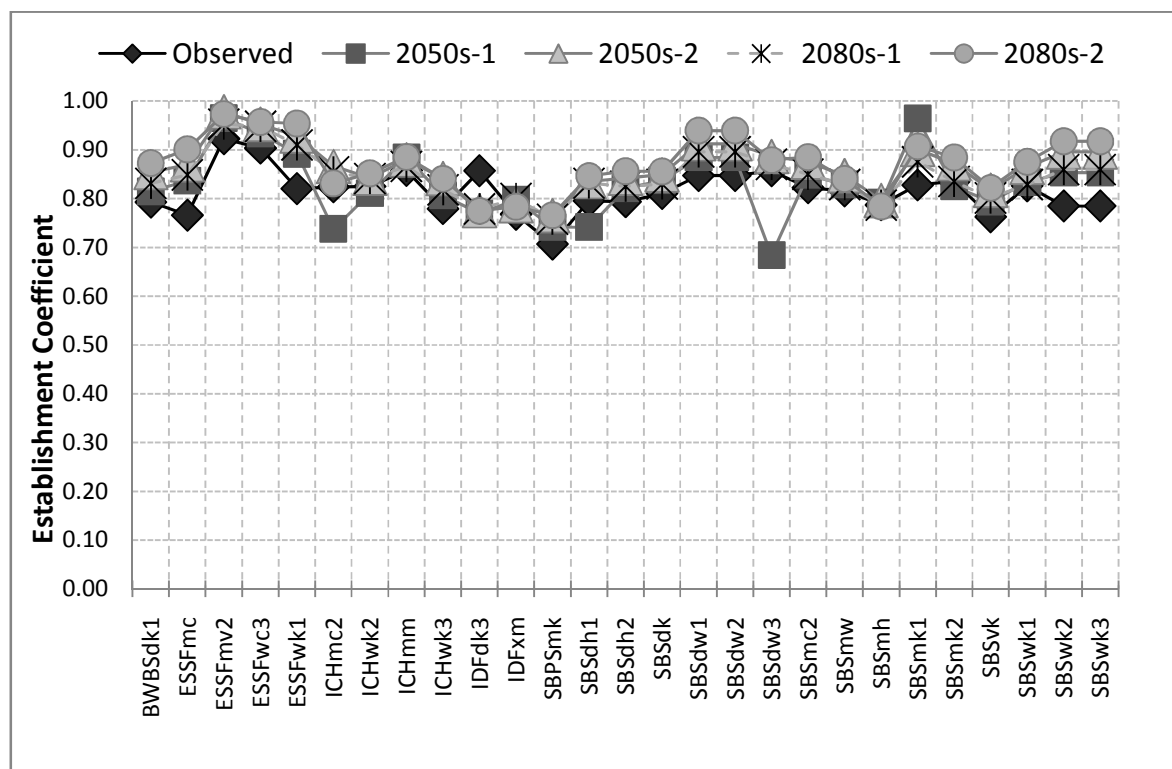


Figure A2b: lodgepole pine response to varying degrees of predicted climate change on mesic sites

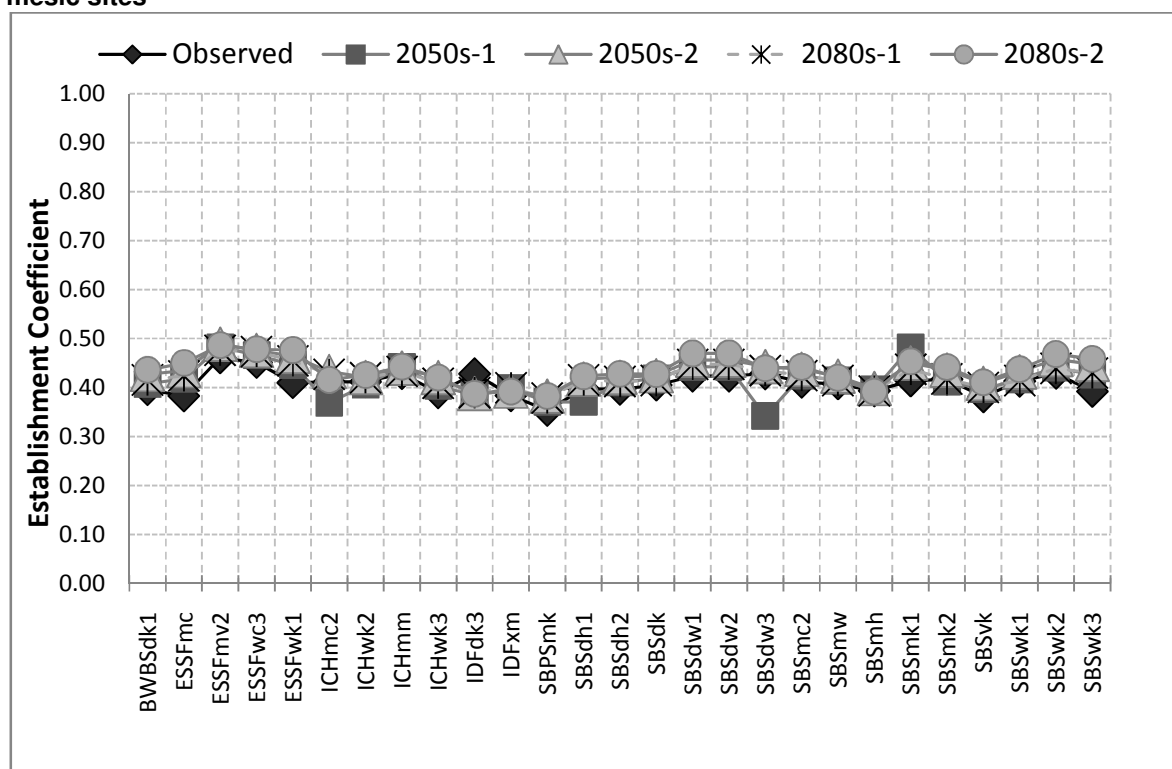


Figure A2c: lodgepole pine response to varying degrees of predicted climate change on moist sites

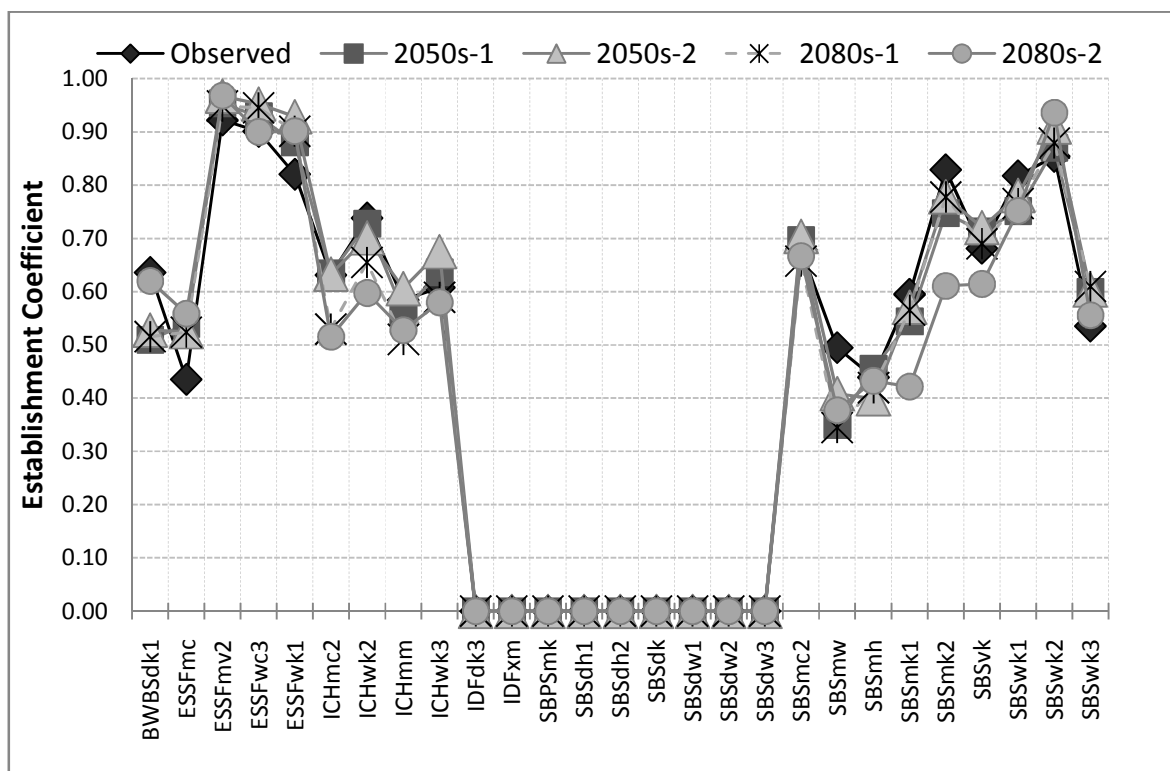


Figure A3a: subalpine fir response to varying degrees of predicted climate change on dry sites

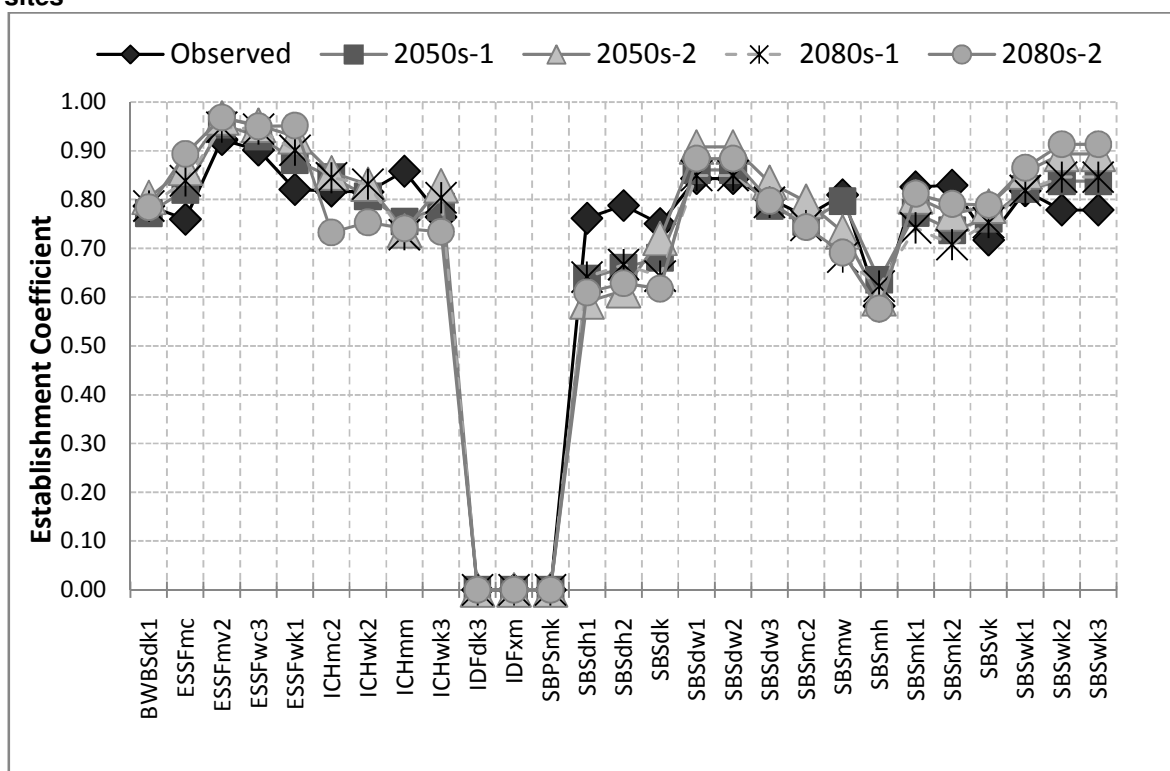


Figure A3b: subalpine fir response to varying degrees of predicted climate change on mesic sites

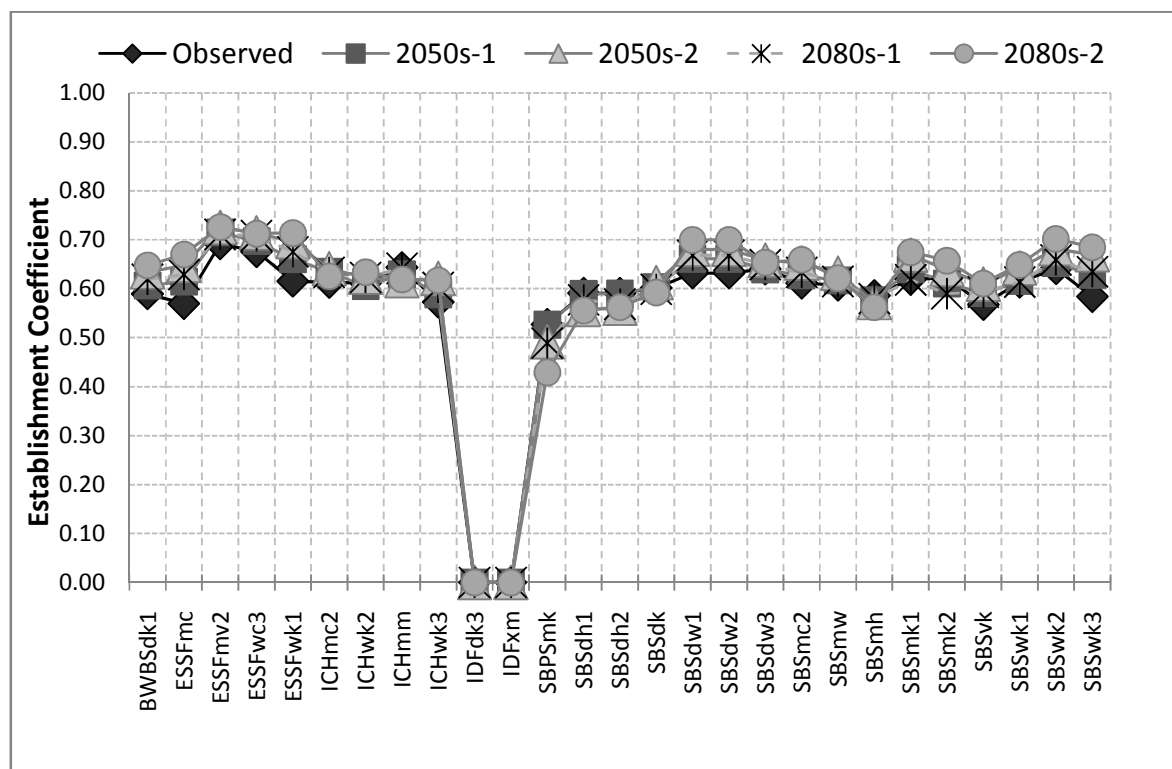


Figure A3c: subalpine fir response to varying degrees of predicted climate change on moist sites

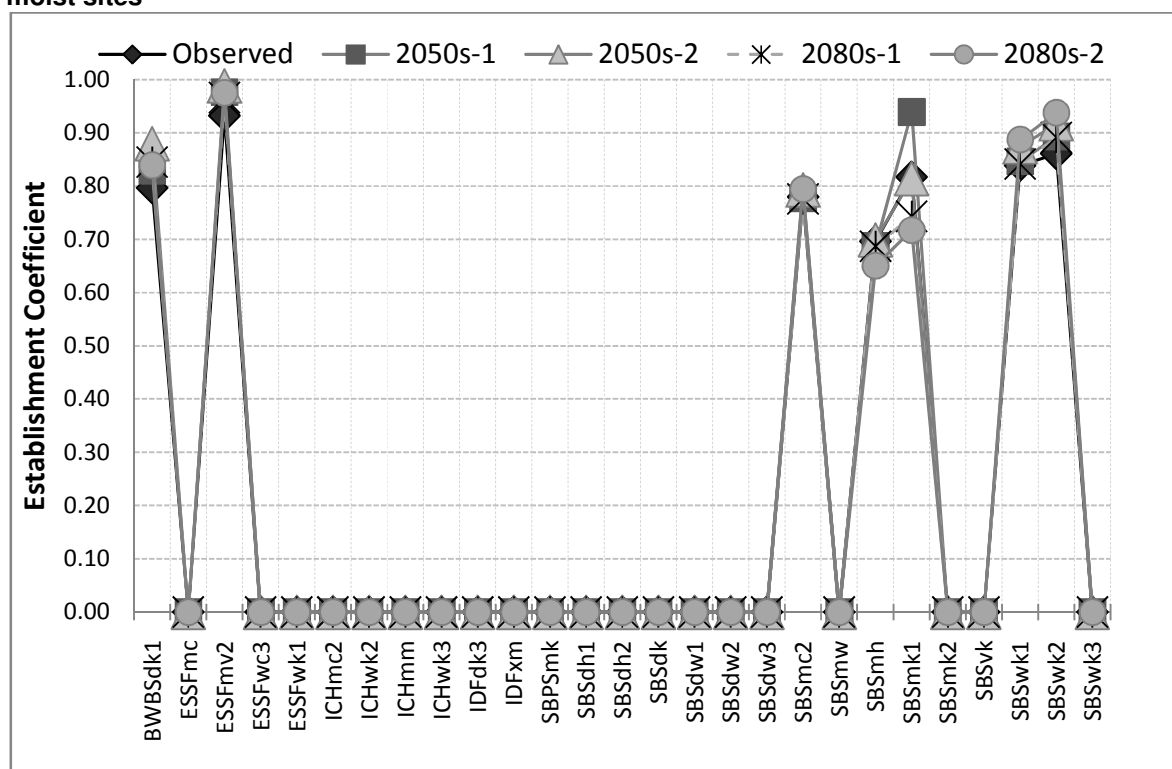


Figure A4a: black spruce response to varying degrees of predicted climate change on dry sites

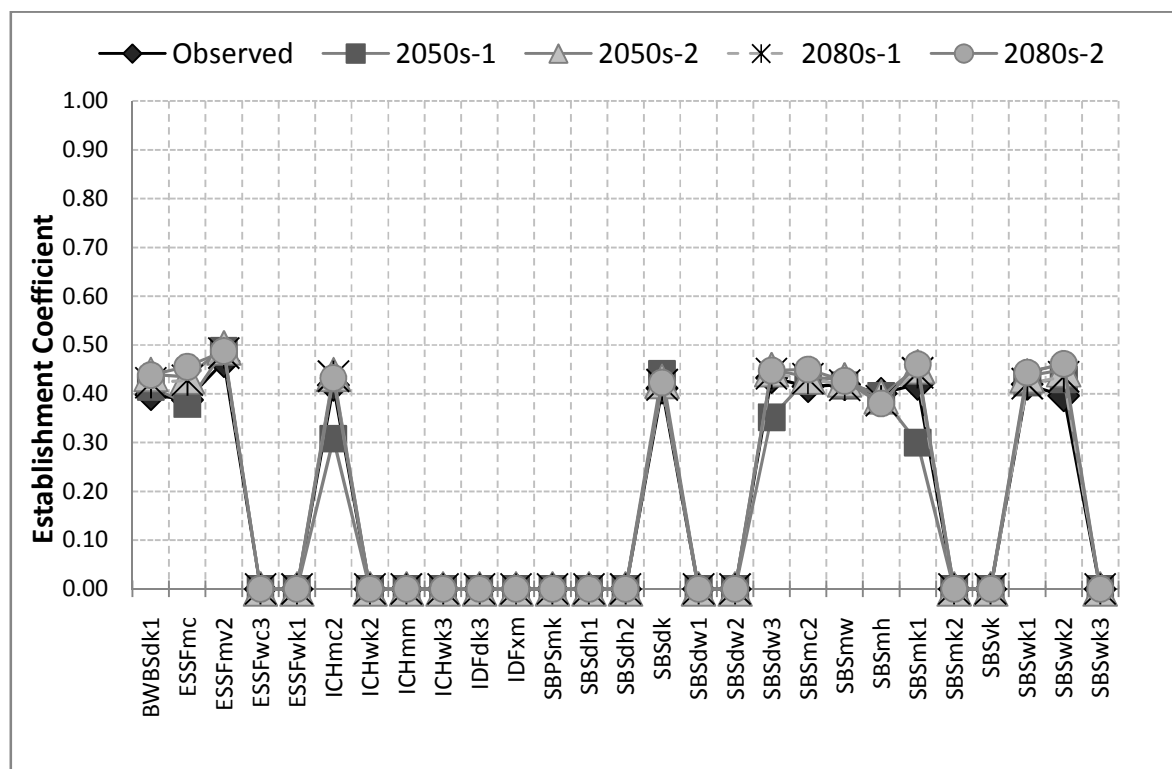


Figure A4b: black spruce response to varying degrees of predicted climate change on mesic sites

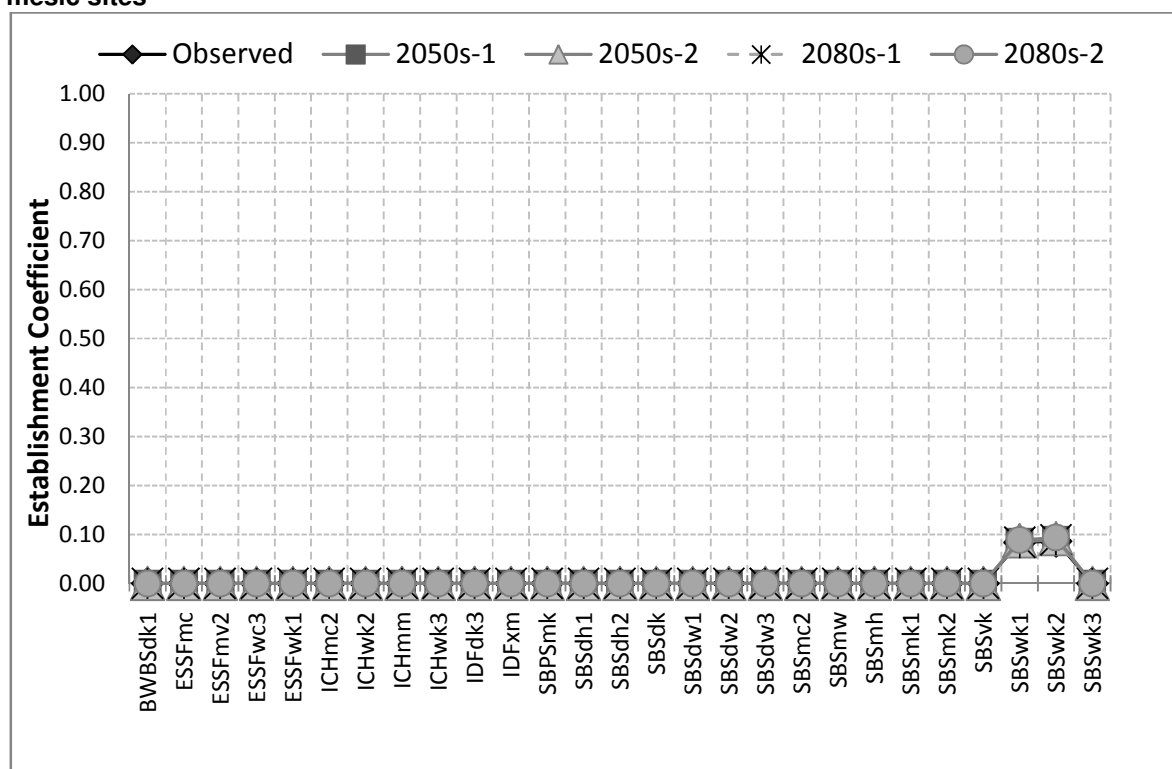


Figure A4c: black spruce response to varying degrees of predicted climate change on moist (rich) sites

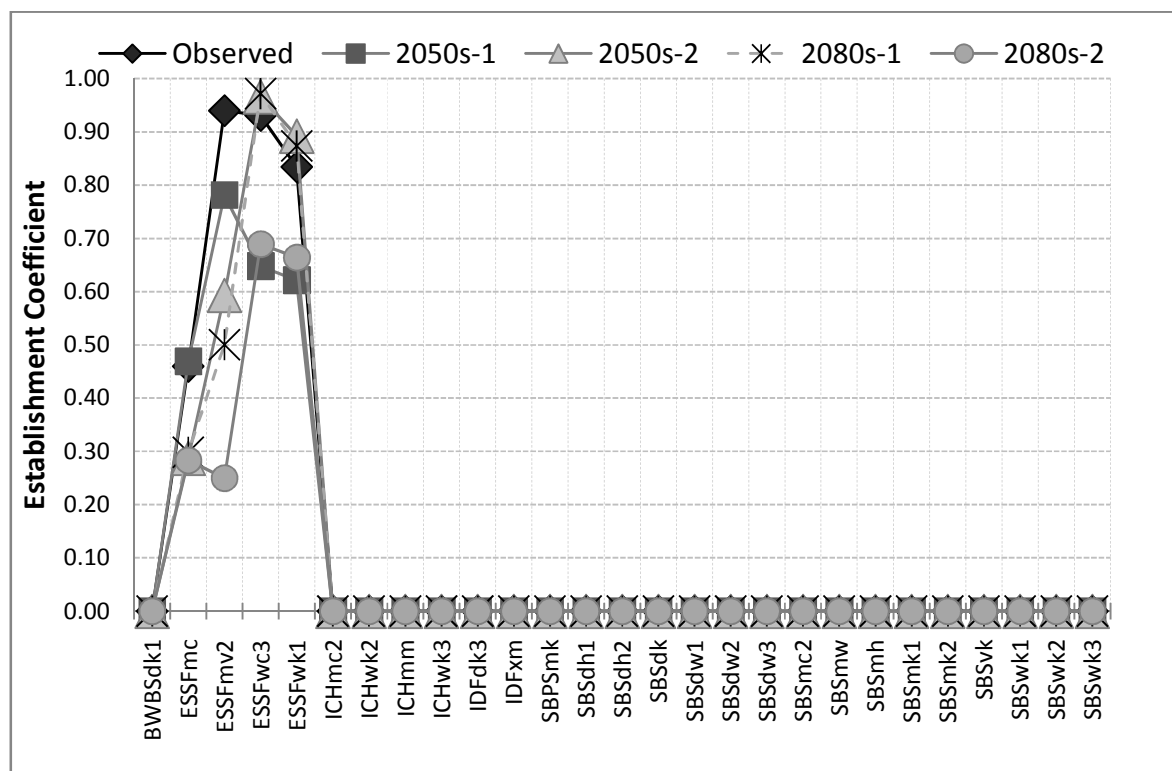


Figure A5a: Engelmann spruce response to varying degrees of predicted climate change on dry sites

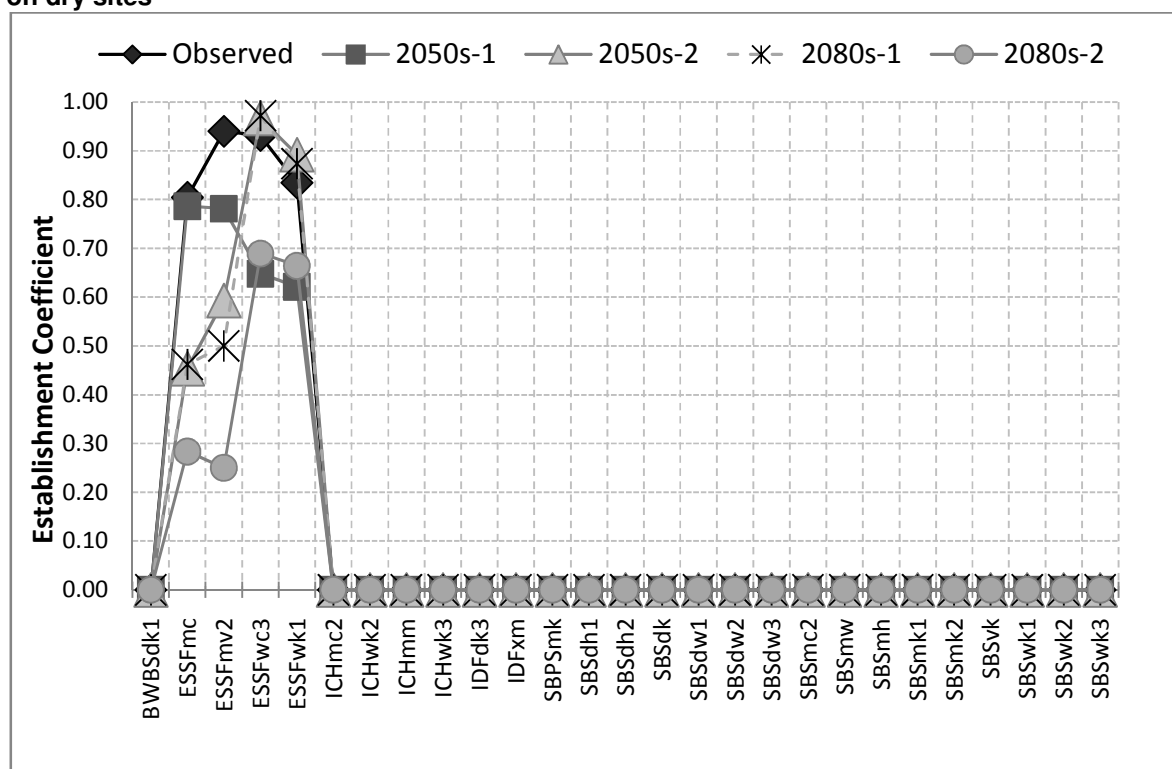


Figure A5b: Engelmann spruce response to varying degrees of predicted climate change on mesic sites

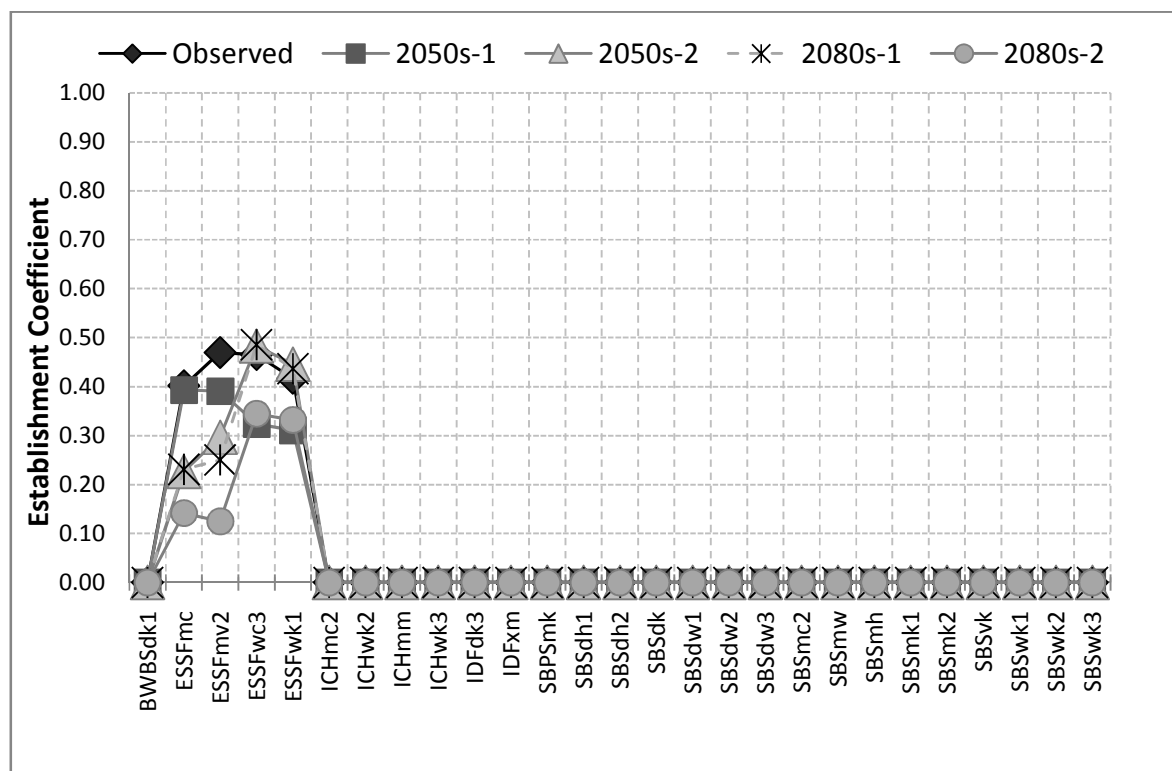


Figure A5c: Engelmann spruce response to varying degrees of predicted climate change on moist sites

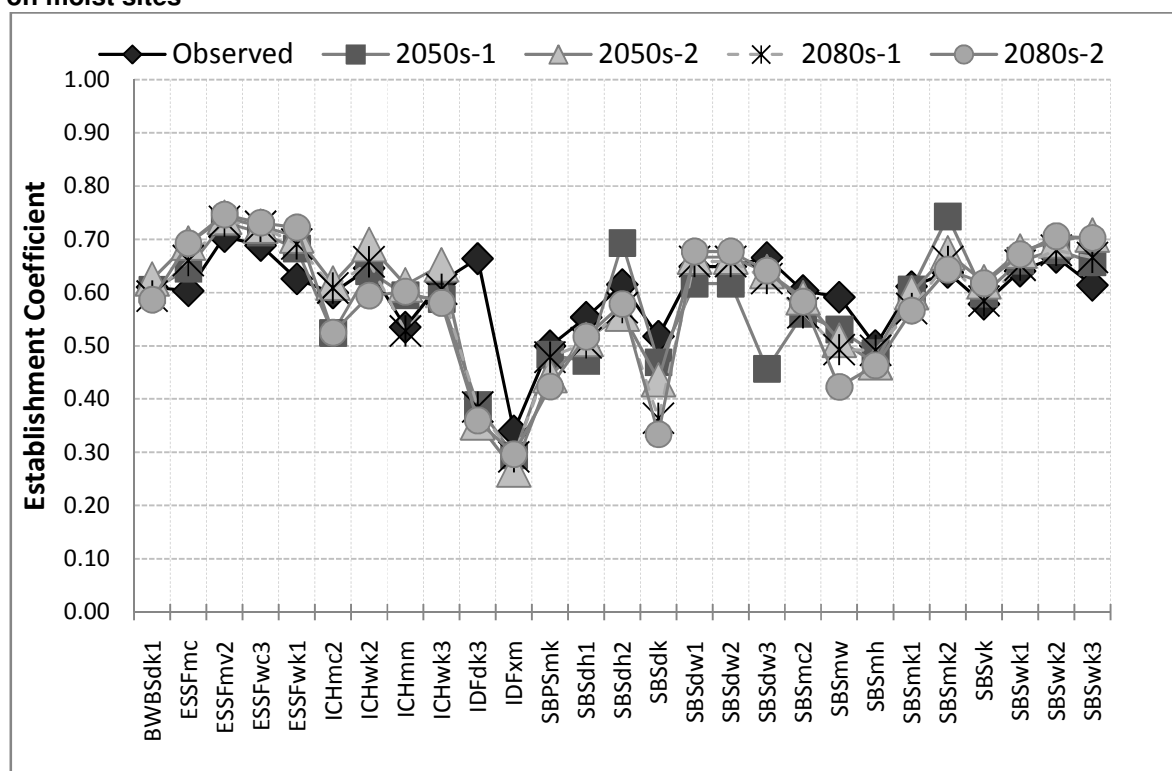


Figure A6a: interior spruce response to varying degrees of predicted climate change on dry sites

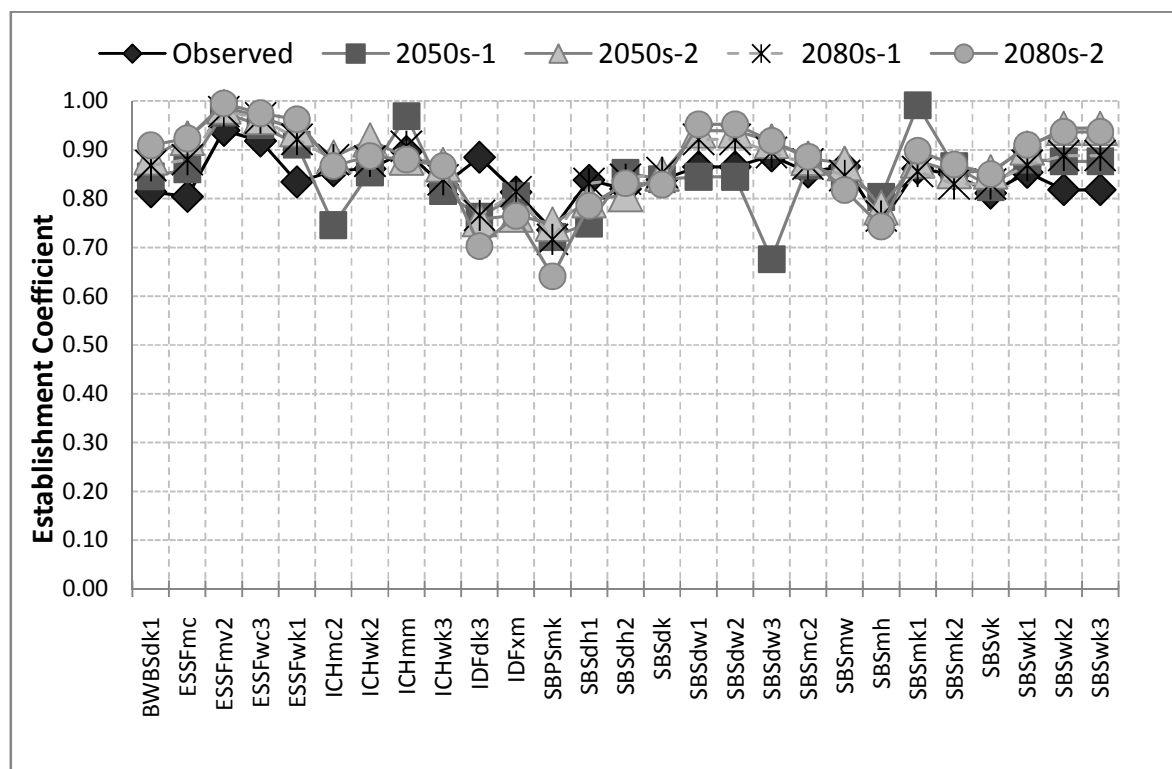


Figure A6b: interior spruce response to varying degrees of predicted climate change on mesic sites

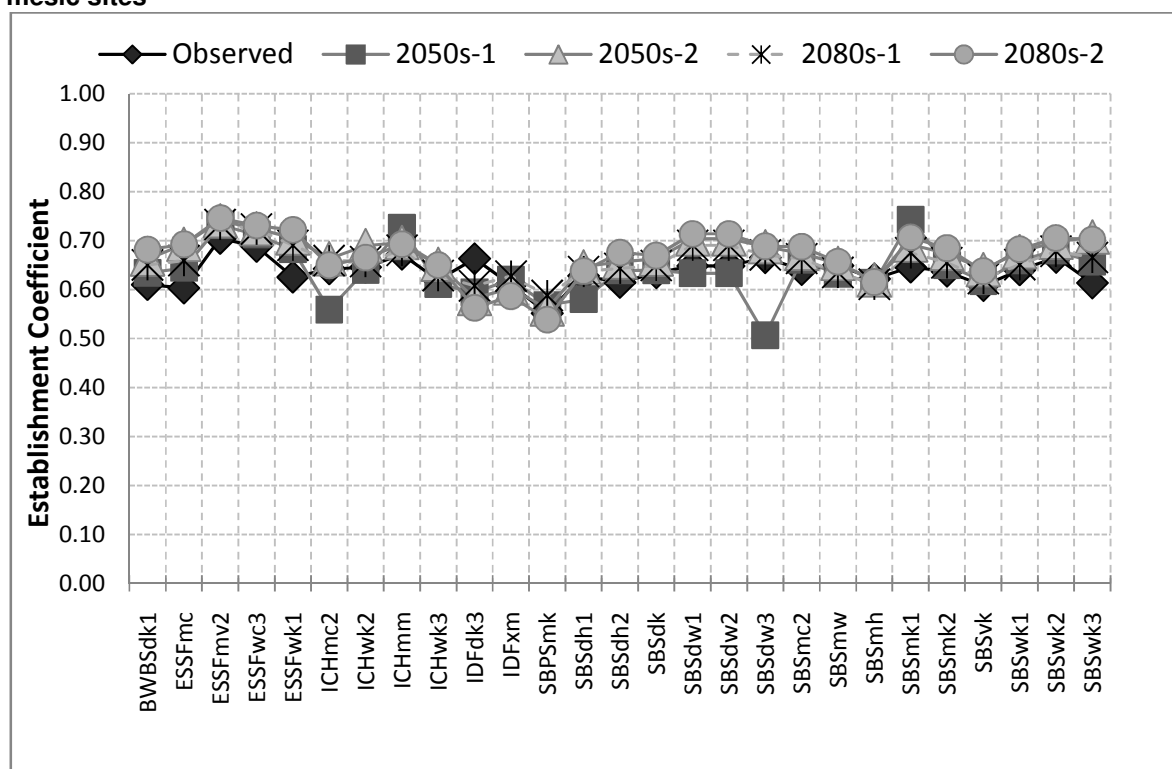


Figure A6c: interior spruce response to varying degrees of predicted climate change on moist sites

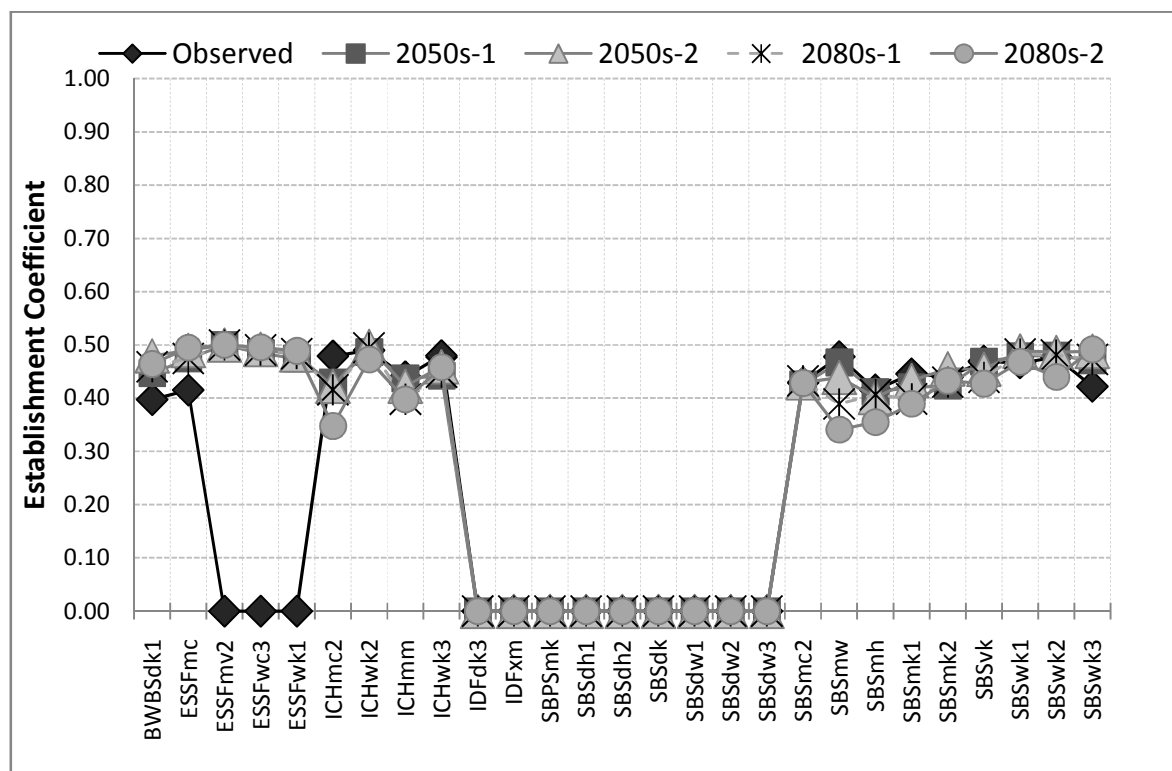


Figure A7a: paper birch response to varying degrees of predicted climate change on dry sites

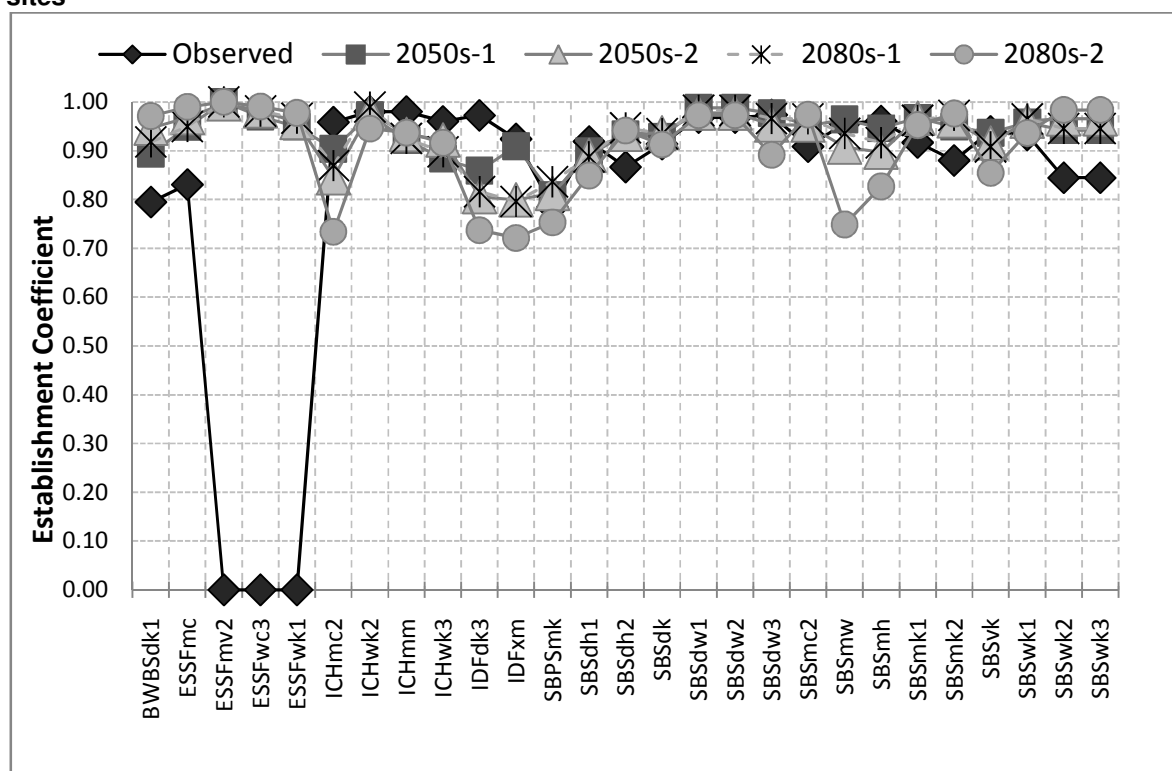


Figure A7b: paper birch response to varying degrees of predicted climate change on mesic sites

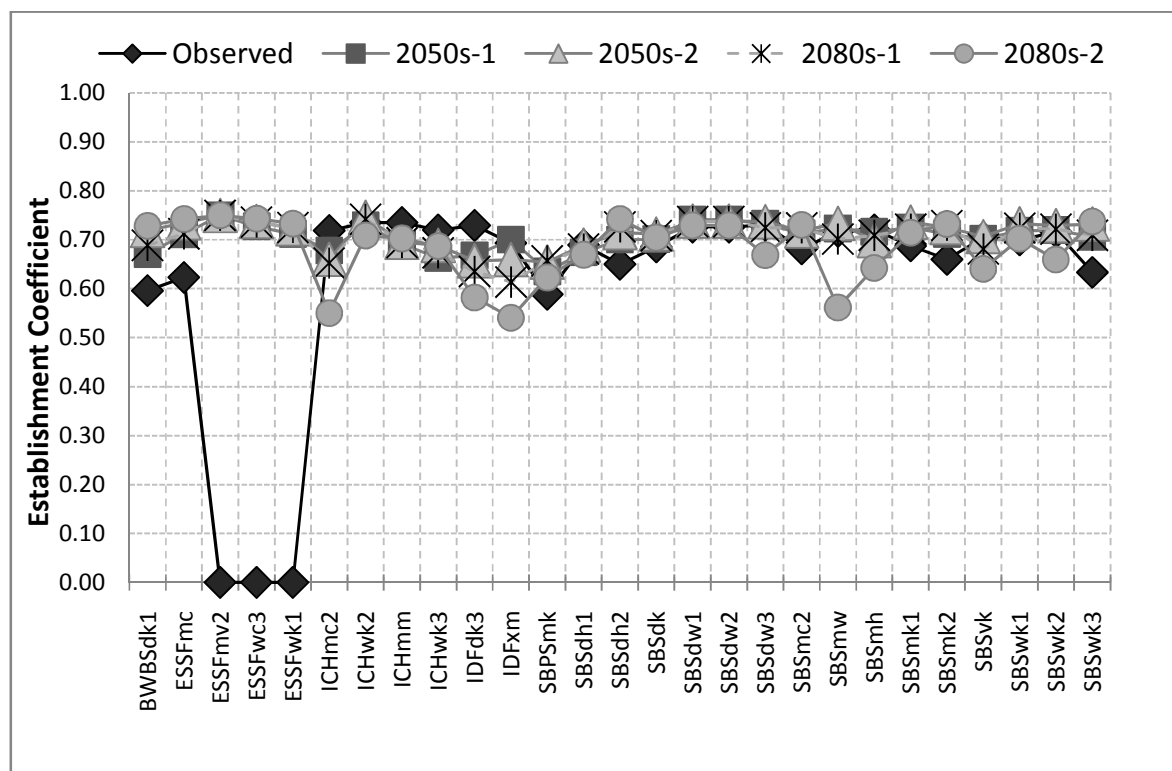


Figure A7c: paper birch response to varying degrees of predicted climate change on moist sites

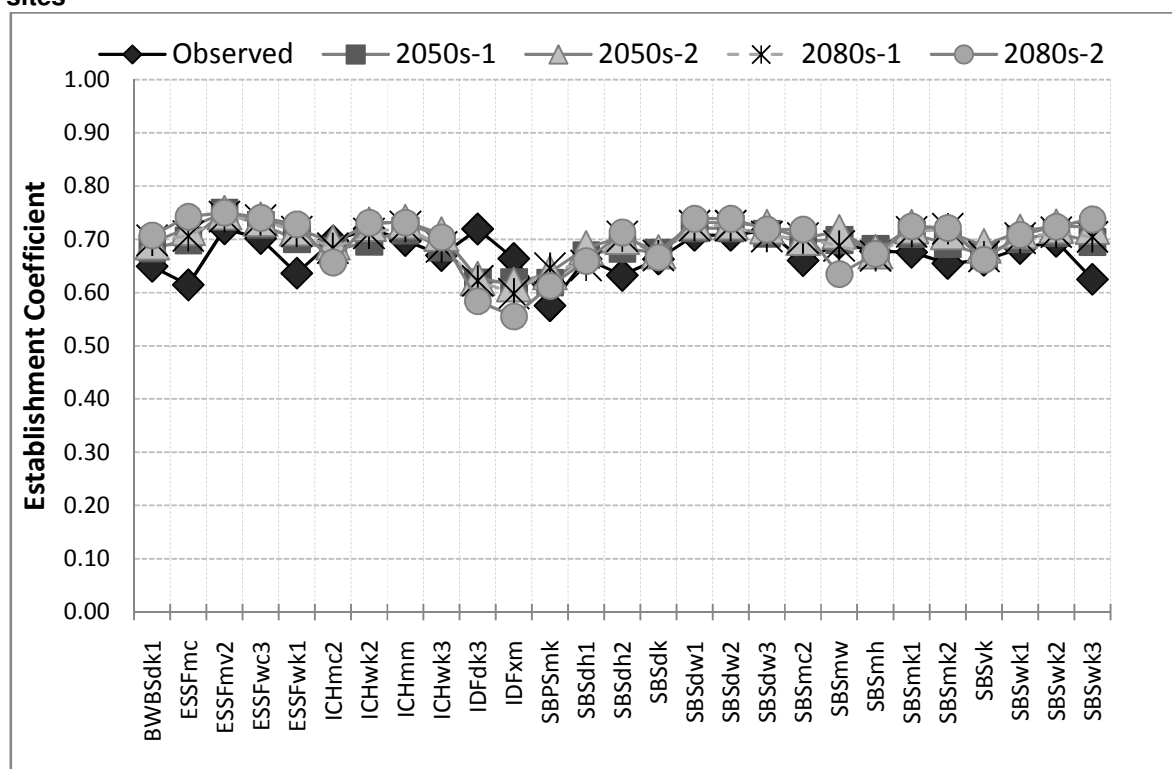


Figure A8a: trembling aspen response to varying degrees of predicted climate change on dry sites

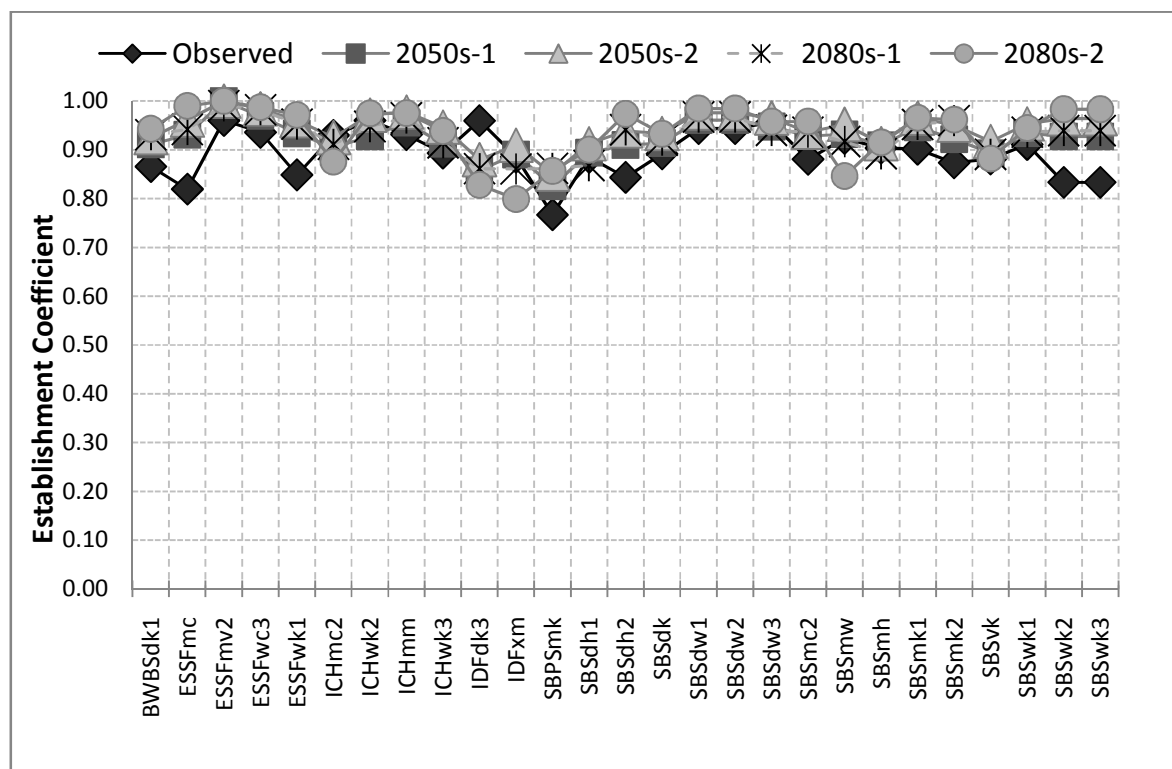


Figure A8b: trembling aspen response to varying degrees of predicted climate change on mesic sites

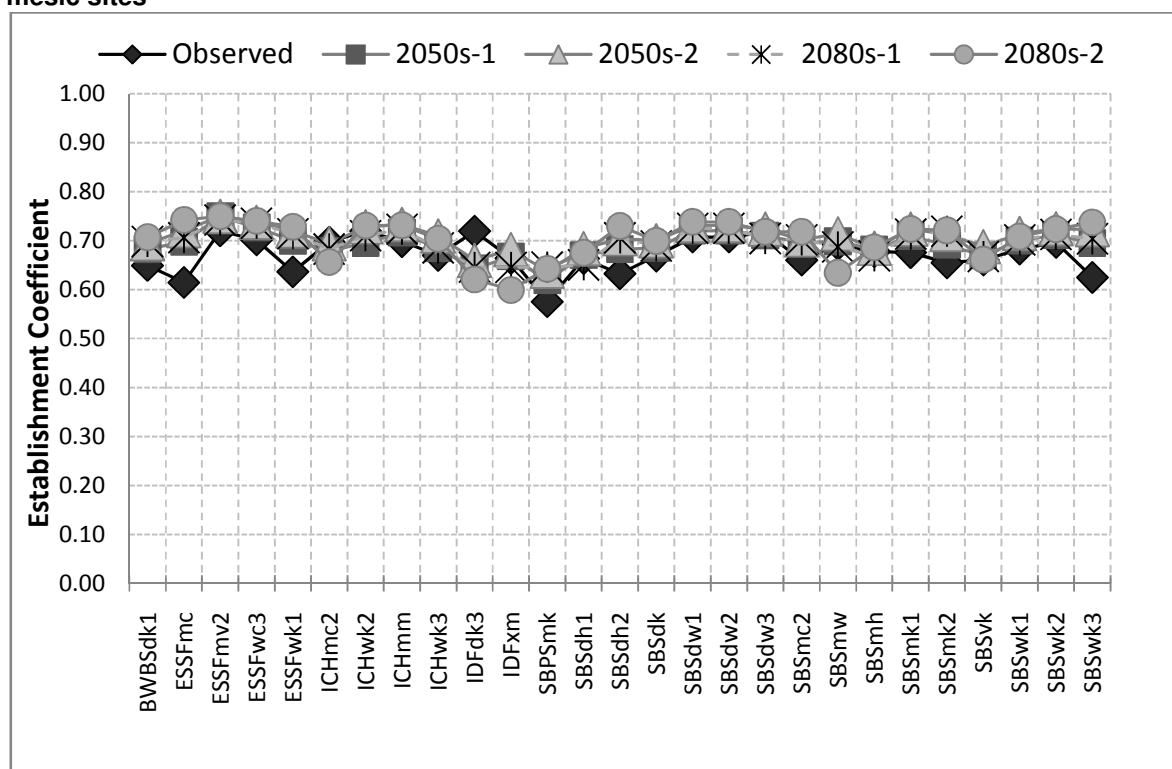


Figure A8c: trembling aspen response to varying degrees of predicted climate change on moist sites

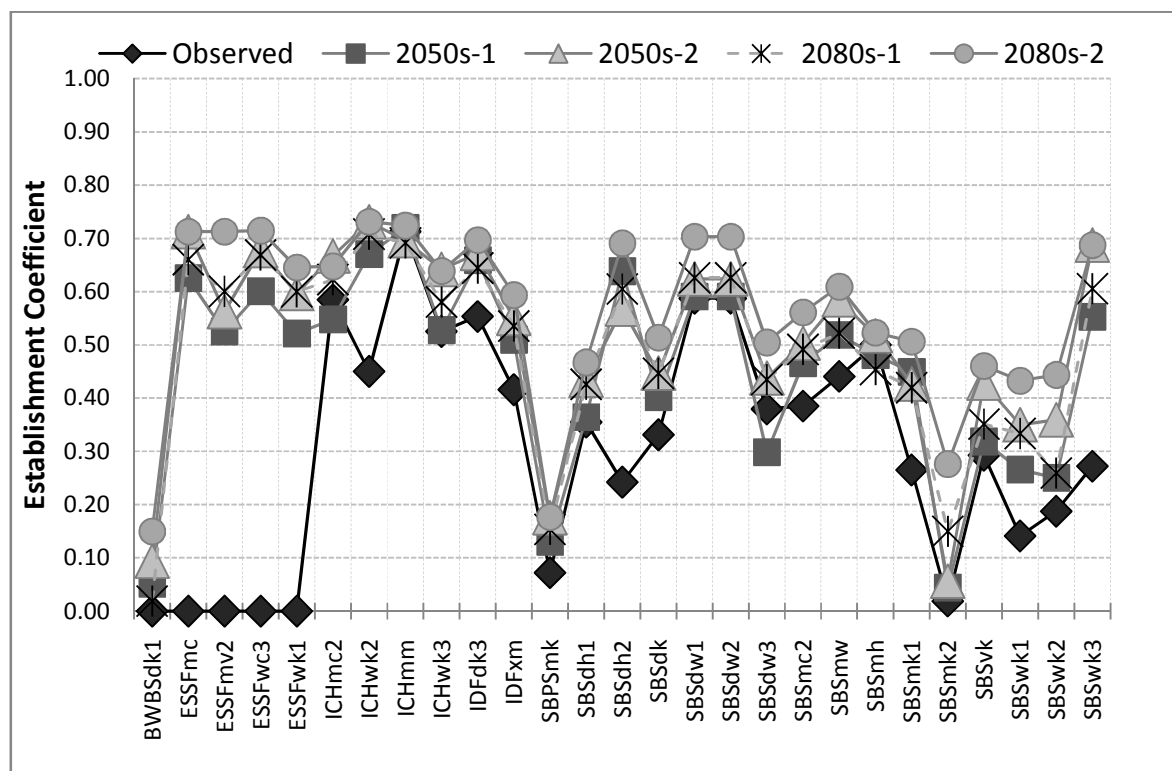


Figure A9a: Douglas-fir response to varying degrees of predicted climate change on dry sites

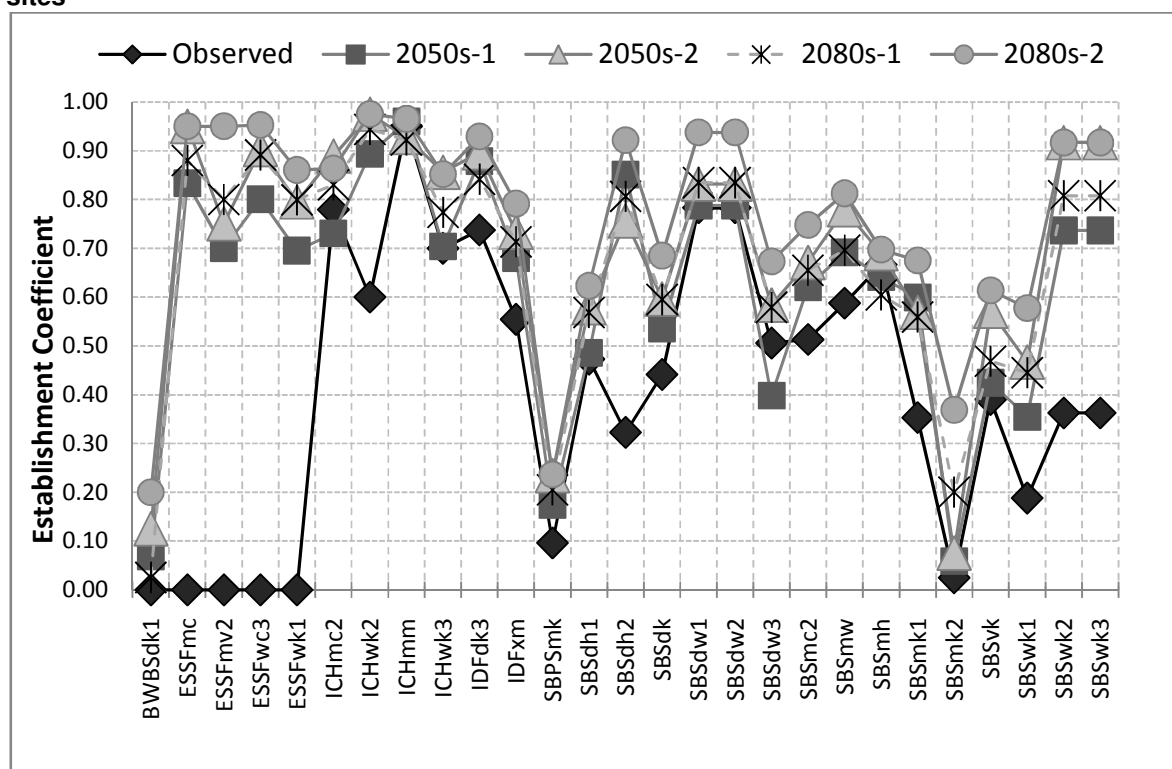


Figure A9b: Douglas-fir response to varying degrees of predicted climate change on mesic sites

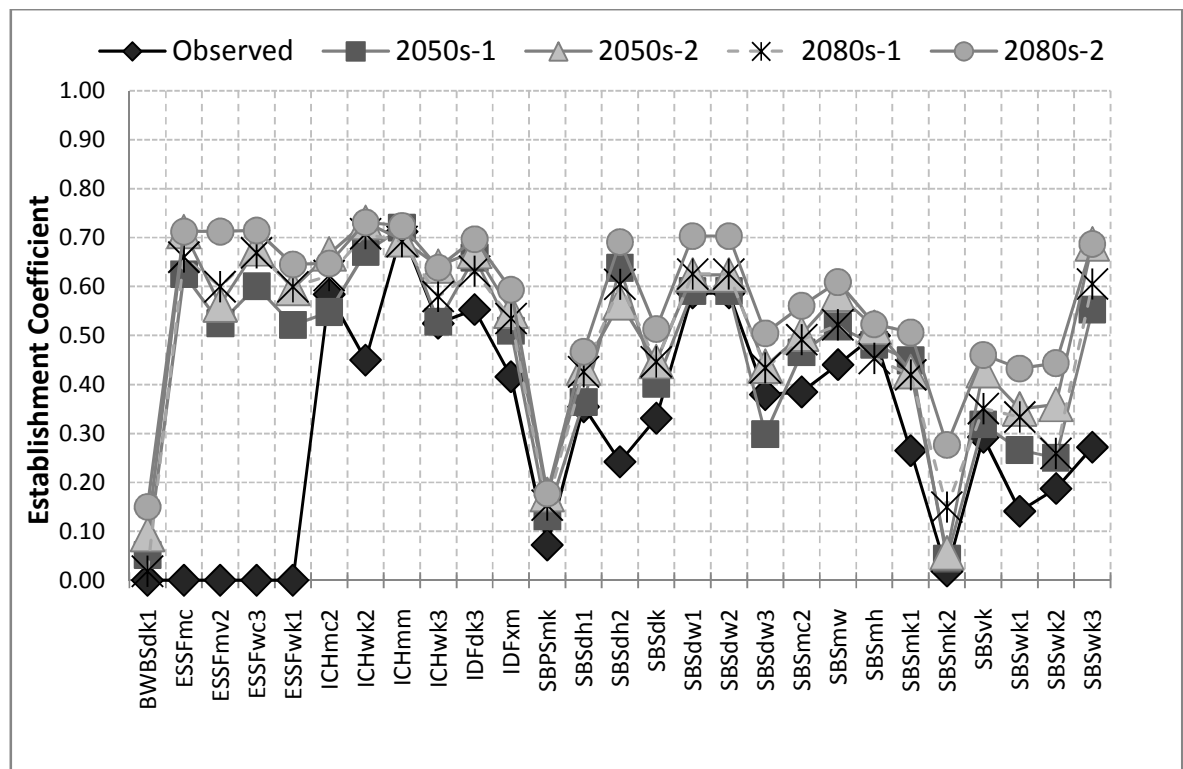


Figure A9c: Douglas-fir response to varying degrees of predicted climate change on moist sites