Response of the cover of berry-producing species to ecological factors on the Kenai Peninsula, Alaska, USA

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Abstract: Land managers on the Kenai Peninsula have responded to recent extensive infestations of forests by spruce beetles (*Dendroctonus rufipennis* (Kirby)) and associated increased fire risk with a variety of management approaches. To provide additional ecological information upon which to base these management prescriptions, we evaluated the response of the cover of berry species to variations in landscape factors and environmental conditions, including crown closure. Data were sufficient to describe the response of cover of bunchberry dogwood (*Cornus canadensis*), black crowberry (*Empetrum nigrum*), false toadflax (*Geocaulon lividum*), strawberryleaf raspberry (*Rubus pedatus*), lingonberry (*Vaccinium vitis-idaea*), and a combination of 24 other species through multinomial logistic regression. Crown closure and forest overstory type significantly influenced the cover of all berry species. Increasing crown closure had a negative effect on all berry species except strawberryleaf raspberry. Level of infestation by spruce beetles was significantly related to the cover of all species except lingonberry. Our findings indicate that spruce forests may be managed to enhance berry cover and that choice of management technique (e.g., timber harvest, prescribed fire) will likely result in different outcomes.

Résumé : Sur la péninsule de Kenai, les aménagistes ont réagi aux grandes infestations récentes des forêts par le dendroctone de l'épinette (*Dendroctonus rufipennis* (Kirby)) et à l'augmentation du risque de feu qui y est associé par une variété d'approches d'aménagement. Afin de fournir de l'information écologique additionnelle pour appuyer ces prescriptions d'aménagement, nous avons évalué la réaction des espèces qui produisent des petits fruits aux variations des facteurs du paysage et des conditions environnementales, incluant la fermeture du couvert forestier. Les données étaient suffisantes pour décrire la réaction du couvert du cornouiller du Canada (*Cornus canadensis*), de la camarine noire (*Empetrum nigrum*), de la comandre livide (*Geocaulon lividum*), du framboisier rampant (*Rubus pedatus*), de l'airelle rouge (*Vaccinium vitis-idaea*) et d'une combinaison de 24 autres espèces au moyen de la régression logistique multinomiale. La fermeture du couvert et le type d'étage dominant arborescent ont significativement influencé la couverture de toutes les espèces qui produisent des petits fruits. L'augmentation de la fermeture du couvert avait un effet négatif sur toutes les espèces qui produisent des petits fruits à l'exception du framboisier rampant. Le degré d'infestation du dendroctone de l'épinette était significativement relié au couvert de toutes les espèces à l'exception de l'airelle rouge. Nos résultats indiquent que les forêts d'épinette peuvent être aménagées pour accroître le couvert d'espèces qui produisent des petits fruits et que le choix de la technique d'aménagement (p. ex. récolte de bois, brûlage dirigé) produira vraisemblablement différents résultats.

[Traduit par la Rédaction]

Introduction

Land managers on Alaska's Kenai Peninsula have responded to recent extensive infestations of forests by spruce beetles (*Dendroctonus rufipennis* (Kirby)) (Holsten et al. 1995; Reynolds and Holsten 1996; Wittwer 2004) and the fire risk associated with the increased volume of standing dead and down woody material with a variety of management approaches. These have included leaving infested stands unmanaged, harvesting dead and live trees to reduce fuels, and applying prescribed burns to consume fuels under controlled conditions. The response of understory plants to various types of disturbance is not as well documented as the response of regenerating trees (Whittle et al. 1997; Kemball et al. 2006). Management of ecosystems such as the eastern Kenai Peninsula requires consideration of all compo-

Received 12 February 2007. Accepted 28 November 2007. Published on the NRC Research Press Web site at cjfr.nrc.ca on 26 April 2008.

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 doi:10.1139/X07-229

nents of the landscape, including the response of berry species to management regimes. Wildlife (e.g., northern red-backed voles (*Clethrionomys rutilus*) (West 1982)) and humans (e.g., berry picking (von Hagen and Fight 1999; Bowker 2001)) directly use berries. The lack of information on response of berry species to natural and human-induced disturbances has been a major impediment to the development of management plans with comprehensive objectives and to evaluations of the effects of proposed management. Understanding the response of berry-producing species to landscape factors and changing environmental conditions associated with prescribed management actions would help in managing the landscape for wildlife species that rely on berries as a food source and for people that utilize berries for subsistence, commercial, or recreation purposes.

As many as 14 species of mammals and 30 species of birds that occur on the Kenai Peninsula commonly feed on berries (Martin et al. 1951; Erhlich et al. 1988). The spruce beetle infestation and subsequent forest management practices have changed the forest canopy structure and directly affected habitats used by many forest birds (Lance and Howell 2000; Matsuoka et al. 2001). Creation of overstory openings resulted in changes in understory vegetation that, in turn, affect habitat used by small mammals (Williams 1999; Matsuoka et al. 2001). Brown bears (*Ursus arctos*) and American black bears (*Ursus americanus*) also eat berry crops during summer and fall (Risdahl 1984; Smith 1984; Schwartz and Franzmann 1991). We previously reported on the effects of the spruce beetle infestation on berry productivity on the Kenai Peninsula (Suring et al. 2006). Here we quantify the cover of berry-producing species and its relationship to stand and landscape characteristics, so that forest management activities could be implemented to benefit berry production. We hypothesized that response of berry cover would vary by forest overstory type and by ecological conditions across the landscape and that manipulation of crown closure would offer a means to manage for berry productivity through silvilcultural practices.

Materials and methods

Study area

Our 500 000 ha study area was located in the Chugach National Forest on the Kenai Peninsula, Alaska, from Portage south to Seward and west to the boundary of the Kenai National Wildlife Refuge. The topography was characterized by rounded to jagged mountains separated by alpine and glacier-shaped valleys; elevations ranged from 30 to 1800 m. The climate is wet and transitional (50–200 cm of annual precipitation) with mild to cool summers and cool winters (4–7 °C mean annual temperature). White spruce (*Picea glauca* (Moench) Voss) and Lutz spruce (*Picea* × *lutzii* Little (*glauca* × *mariana*)) dominated on valley bottoms and side slopes, while mountain hemlock (*Tsuga mertensiana* (Bong.) Carrière) occurred primarily on side slopes at low to mid elevations. Mixed conifer–deciduous forests had paper birch (*Betula papyrifera* Marsh.) as a major component. Valley bottoms commonly supported black cottonwood (*Populus trichocarpa* Torr. & A. Gray), and willow (*Salix* spp.). Understory species found throughout the study area included bluejoint (*Calamagrostis canadensis*), rusty menziesia (*Menziesia ferruginea*), oval-leaf blueberry (*Vaccinium ovalifolium)*, devilsclub (*Oplopanax horridus)*, lingonberry (*Vaccinium vitis-idaea)*, and black crowberry (*Empetrum nigrum)*. Thirty-two species of berry-producing shrubs and forbs have been documented on the study area, of which 20 occur commonly (DeVelice et al. 1999).

Sampling sites and sample size

Land type associations (a landscape unit formed and influenced by similar geomorphic processes) and land types (a landscape unit with more detail than land type association having one major geomorphic process, one major landform, and a complex of soils and plant communities) (D. Davidson, Chugach National Forest, unpublished data 1999) provided a framework for sampling vegetation. Land type associations included mountain slopes, hills, and lowlands. Land types included frequently dissected, deeply incised mountain slopes; frequently dissected, shallowly incised mountain slopes; forested lower side slopes; nonforested lower side slopes; alluvial fans; braided rivers; marine terraces; high-relief terraces; low-relief hills; and high-relief hills. We sampled sites dominated by white spruce, Lutz spruce, white and Lutz spruce with mountain hemlock, and mountain hemlock within these areas.

We used a geographic information system to establish a grid with 400 m × 400 m cells across a map of the study area. Grid intersections in white spruce, Lutz spruce, white and Lutz spruce with mountain hemlock, or mountain hemlock sites provided 339 potential starting points for line transects. We established 96 transects (46 in 1999 and 50 in 2000) from randomly selected starting points across this grid. We established a line transect in a random direction at each starting point, established the first sample plot randomly between 1 and 20 m from the initiation point on each transect, and established nine additional sample plots at 20 m intervals along the transect.

Data collection

We used a 1 m^2 rectangular frame to delineate the sample plots (Cherkasov 1974; Smith 1984). At each sample plot, we visually estimated and recorded the proportion of the plot covered by each berry-producing species as a cover class (i.e., 0%; 1%–5%, 6%–15%, 16%–25%, 26%–35%, 36%–45%, 46%–55%, 56%–65%, 66%–75%, 76%–95%, 96%–100%), proportion of other vegetation, and proportion of non-vegetation summing to 100%. We recorded an image of the overstory crown closure at each sample plot using a digital camera with a 37 mm wide-angle lens at a standard height, similar to the method of Kirchhoff and Thomson (1998). We estimated the proportion of beetle-infested white and Lutz spruce trees ≥15 cm diameter at breast height within 10 m of the sample plot as low (1%–10%), medium (11%–40%), or high (>40%) compared with all white and Lutz spruce present.

Data analysis

We used cover categories of the five berry species that occurred most frequently on sampled plots (i.e., bunchberry dogwood, black crowberry, false toadflax, strawberryleaf raspberry, and lingonberry) as response variables in separate regression analyses. Markedly, these most common species were absent from 45%–77% of plots. Observations in the

Table 1. Combined cover classes for analysis of berry-producing plants on the Kenai Peninsula, Alaska.

Percentage of cover	No. of observations
Bunchberry dogwood	
0 (p_1)	473
1–5 (p_2)	305
6–15 (p_3)	96
16–100 (p_4)	113
Black crowberry	
0 (p_1)	733
1–25 (p_2)	138
26–100 (p_3)	116
False toadflax	
0 (p_1)	758
1–5 (p_2)	141
6–100 (p_3)	88
Strawberryleaf raspberry	
0 (p_1)	446
1–5 (p_2)	252
6–15 (p_3)	142
16–100 (p_4)	147
Lingonberry	
0 (p_1)	619
1–5 (p_2)	231
6–100 (p_3)	135
Other berries	
0 (p_1)	456
0^+–5 (p_2)	161
5^+–15 (p_3)	142
15^+–138 (p_4)	228

"higher" cover classes were infrequent, so classes were collapsed to create either three or four categories, depending on species (Table 1). Because each of the remaining berry species was absent from ≥91% of plots (Table 2), we established an additional response variable, other_berry_cover. This variable was created by converting the assigned cover category for each species to the midpoint of the corresponding percentage cover range. Then, these midpoint values were summed across species as if these values were observations on continuous variables. This sum was treated as a continuous explanatory variable (other_berry_cover) in regressions when cover of one of the five primary species was analyzed as the response variable. Combined cover of species other than the five primary species was also modeled as a response variable by back-converting the sums of midpoints into four categories.

We considered the following environmental covariates as potential explanatory variables for the cover of the berry species evaluated: crown closure, overstory type, infestation level, land type, and land type association. We measured crown closure using the digital images (proportion of covered pixels), and created another variable by calculating the quadratic of canopy closure. We collapsed the overstory vegetation types into four categories: white spruce, white spruce – mountain hemlock, Lutz spruce (representing all types in which Lutz spruce had the highest cover of any of the tree species present), and mountain hemlock (representing all types in which mountain hemlock had the highest cover of any of the tree species present).

Table 2. Berry-producing shrubs and forbs documented to occur on the eastern Kenai Peninsula, Alaska, and included in this analysis (adapted from DeVelice et al. 1999).

Common name	Scientific name	Occurrence
Red fruit bearberry	*Arctostaphylos rubra*	Rare
Kinnikinnick	*Arctostaphylos uva-ursi*	Rare
Bunchberry dogwood	*Cornus canadensis*	Common
Devilsclub	*Oplopanax horridus*	Common
Black crowberry	*Empetrum nigrum*	Common
False toadflax	*Geocaulon lividum*	Common
Small cranberry	*Vaccinium oxycoccos*	Common
Stink current	*Ribes bracteosum*	Rare
Skunk currant	*Ribes glandulosum*	Rare
Northern black currant	*Ribes hudsonianum*	Rare
Trailing black currant	*Ribes laxiflorum*	Common
Currant	*Ribes species*	—
Red currant	*Ribes triste*	Common
Prickly rose	*Rosa acicularis*	Common
Arctic blackberry	*Rubus arcticus*	Common
Cloudberry	*Rubus chamaemorus*	Rare
American red raspberry	*Rubus idaeus*	Rare
Strawberryleaf raspberry	*Rubus pedatus*	Common
Salmonberry	*Rubus spectabilis*	Common
Red elderberry	*Sambucus racemosa*	Common
Russet buffaloberry	*Shepherdia canadensis*	Rare
Greene's mountain ash	*Sorbus scopulina*	Common
Sitka mountain ash	*Sorbus sitchensis*	Common
Claspleaf twistedstalk	*Streptopus amplexifolius*	Common
Dwarf bilberry	*Vaccinium caespitosum*	Rare
Oval-leaf blueberry	*Vaccinium ovalifolium*	Common
Bog blueberry	*Vaccinium uliginosum*	Common
Lingonberry	*Vaccinium vitis-idaea*	Common
Squashberry	*Viburnum edule*	Common

Note: Plant nomenclature follows USDA Natural Resources Conservation Service (2004).

We constructed cover of understory vegetation other than the response variables as three alternative explanatory variables: vegetation other than berry species (designated other_veg), other_berry_cover, and total other cover (designated other_cover). Before summing, we converted cover classes to the mid-points of the corresponding ranges of cover values. We included each of these three variables in regression analyses, though no two were included simultaneously in any model. We did not consider other_berry_cover as an explanatory variable when other berry species was the response variable. We analyzed infestation level as low, medium, or high. To simplify analyses, we collapsed the land type categories that were ecologically similar: frequently dissected, deeply incised mountain slopes with frequently dissected, shallowly incised mountain slopes; alluvial fans with braided rivers; marine terraces with high-relief terraces; and low-relief hills with high-relief hills.

We sorted potential explanatory variables into three groups from the most to the least responsive to management actions (e.g., management actions could influence crown closure but could not affect land types): (*i*) crown closure

Table 3. Final multinomial logit models for cover by berry species, on the eastern Kenai Peninsula, Alaska.

Parameter	Value cover logit	Estimate	SE	χ^2	*P*
Bunchberry dogwood					
Crown closure	p_1/p_4	–0.0411	0.0178	7.97	0.047
	p_2/p_4	–0.0266	0.0183		
	p_3/p_4	–0.0048	0.0224		
Other berry cover	p_1/p_4	0.0252	0.0085	25.43	<0.001
	p_2/p_4	0.0040	0.0092		
	p_3/p_4	–0.0029	0.0123		
Overstory[a]					
White spruce	p_1/p_4	–2.2790	0.4801	28.61	<0.001
	p_2/p_4	–1.4454	0.4820		
	p_3/p_4	–0.8486	0.5759		
White spruce – hemlock	p_1/p_4	–0.9817	0.4855	6.07	0.108
	p_2/p_4	–1.2294	0.5031		
	p_3/p_4	–1.0409	0.6007		
Lutz spruce	p_1/p_4	–1.6034	0.4254	19.73	<0.001
	p_2/p_4	–1.2334	0.4368		
	p_3/p_4	–0.5447	0.5116		
Infestation[b]					
Low	p_1/p_4	–1.4652	0.3293	24.81	<0.001
	p_2/p_4	–0.8602	0.3308		
	p_3/p_4	–0.5617	0.3897		
Medium	p_1/p_4	–1.1127	0.3469	10.79	0.013
	p_2/p_4	–1.0708	0.3645		
	p_3/p_4	–0.9837	0.4635		
Land type[c]					
Mountain slopes	p_1/p_4	–1.7701	0.6728	9.89	0.020
	p_2/p_4	–2.2181	0.7153		
	p_3/p_4	–1.4682	0.7949		
Forested slopes	p_1/p_4	0.6702	0.8161	3.56	0.313
	p_2/p_4	0.1997	0.8463		
	p_3/p_4	–0.9482	1.2766		
Nonforested slopes	p_1/p_4	–2.0236	0.5571	14.83	0.002
	p_2/p_4	–1.8643	0.5977		
	p_3/p_4	–1.6301	0.7613		
Fans or rivers	p_1/p_4	–1.9109	0.5656	12.67	0.005
	p_2/p_4	–1.0887	0.4862		
	p_3/p_4	–0.4793	0.5465		
Plateaus	p_1/p_4	–1.1021	0.5440	12.18	0.007
	p_2/p_4	–2.1655	0.6572		
	p_3/p_4	–1.9580	0.8935		
Terraces	p_1/p_4	–0.4351	0.3406	3.08	0.379
	p_2/p_4	–0.5454	0.3472		
	p_3/p_4	–0.6534	0.4109		
Black crowberry					
Crown closure	p_1/p_3	–0.0233	0.0169	4.71	0.095
	p_2/p_3	0.0064	0.0199		
Other berry cover	p_1/p_3	0.0536	0.0131	24.64	<0.001
	p_2/p_3	0.0274	0.0144		
Overstory[a]					
White spruce	p_1/p_3	–1.1537	0.3858	13.35	0.001
	p_2/p_3	–0.2283	0.4205		
White spruce – hemlock	p_1/p_3	0.1983	0.4031	1.27	0.531
	p_2/p_3	–0.1583	0.4777		
Lutz spruce	p_1/p_3	–1.0584	0.3444	11.47	0.003
	p_2/p_3	–1.2892	0.4175		
Infestation[b]					
Low	p_1/p_3	–1.1219	0.2850	18.14	<0.001

Table 3 (*continued*).

Parameter	Value cover logit	Estimate	SE	χ^2	*P*
	p_2/p_3	–0.3696	0.3220		
Medium	p_1/p_3	0.2924	0.3470	1.18	0.554
	p_2/p_3	0.0254	0.4276		
Land type association[d]					
Mountain slopes	p_1/p_3	1.8360	0.6605	7.73	0.005
	p_2/p_3	—	—		
Hills, high relief	p_1/p_3	0.4660	0.2697	3.04	0.218
	p_2/p_3	0.2908	0.3151		
Volcanic	p_1/p_3	1.4494	0.5361	7.80	0.020
	p_2/p_3	0.9108	0.6230		
False toadflax					
Crown closure	p_1/p_3	–0.0560	0.0194	10.32	0.006
	p_2/p_3	–0.0268	0.0227		
Other berry cover	p_1/p_3	0.0827	0.0206	34.50	<0.001
	p_2/p_3	0.0281	0.0229		
Overstory[a]					
White spruce	p_1/p_3	–0.9808	0.4314	18.03	0.000
	p_2/p_3	0.3242	0.4778		
White spruce – hemlock	p_1/p_3	0.1634	0.4256	0.42	0.812
	p_2/p_3	–0.0271	0.5080		
Lutz spruce	p_1/p_3	–0.8122	0.3516	6.73	0.035
	p_2/p_3	–1.0886	0.4520		
Infestation[b]					
Low	p_1/p_3	–0.0502	0.3272	5.15	0.076
	p_2/p_3	–0.6749	0.3917		
Medium	p_1/p_3	–0.4804	0.3322	3.54	0.170
	p_2/p_3	–0.7539	0.4047		
Land type association[d]					
Mountain slopes	p_1/p_3	2.3951	1.0448	5.67	0.059
	p_2/p_3	1.9551	1.1647		
Hills, high relief	p_1/p_3	0.2833	0.2927	2.21	0.331
	p_2/p_3	0.5225	0.3522		
Volcanic	p_1/p_3	0.3906	0.5099	1.29	0.524
	p_2/p_3	–0.2174	0.7928		
Strawberryleaf raspberry					
Crown closure	p_1/p_4	–0.0294	0.0052	37.79	<0.001
	p_2/p_4	–0.0150	0.0052		
	p_3/p_4	–0.0133	0.0058		
Other berry cover	p_1/p_4	0.0180	0.0070	19.07	<0.001
	p_2/p_4	0.0085	0.0073		
	p_3/p_4	–0.0146	0.0097		
Overstory[a]					
White spruce	p_1/p_4	0.1374	0.4700	20.31	<0.001
	p_2/p_4	–1.4214	0.5071		
	p_3/p_4	–0.4095	0.5595		
White spruce – hemlock	p_1/p_4	–0.0415	0.3532	9.33	0.025
	p_2/p_4	–0.6635	0.3336		
	p_3/p_4	0.1994	0.3645		
Lutz spruce	p_1/p_4	2.2269	0.4196	55.90	<0.001
	p_2/p_4	0.7519	0.4275		
	p_3/p_4	0.1797	0.4885		
Infestation[b]					
Low	p_1/p_4	–0.5401	0.3091	16.39	0.001
	p_2/p_4	0.0936	0.2986		
	p_3/p_4	0.6902	0.3493		
Medium	p_1/p_4	–0.4939	0.3603	17.82	0.001
	p_2/p_4	–0.6544	0.3710		

Table 3 (*continued*).

Parameter	Value cover logit	Estimate	SE	χ^2	*P*
	p_3/p_4	0.7417	0.4003		
Land type association[d]					
Mountain slopes	p_1/p_4	–3.8094	0.9057	21.37	<0.001
	p_2/p_4	–1.9640	0.9090		
	p_3/p_4	–1.3055	0.9718		
Hills, high relief	p_1/p_4	–1.0474	0.6331	10.24	0.017
	p_2/p_4	0.1553	0.6074		
	p_3/p_4	0.3009	0.6683		
Volcanic	p_1/p_4	–2.5947	0.8292	12.83	0.005
	p_2/p_4	–1.9100	0.8080		
	p_3/p_4	–0.7071	0.8753		
Land type[c]					
Mountain slopes	p_1/p_4	2.9938	1.1006	7.72	0.052
	p_2/p_4	1.6243	1.0118		
	p_3/p_4	2.0374	1.0722		
Forested slopes	p_1/p_4	1.4058	0.7796	7.68	0.053
	p_2/p_4	–0.1183	0.7692		
	p_3/p_4	0.3625	0.8279		
Nonforested slopes	p_1/p_4	1.5090	0.9436	3.24	0.356
	p_2/p_4	1.1262	0.8636		
	p_3/p_4	0.5281	0.9439		
Fans or rivers	p_1/p_4	1.1173	0.7657	11.16	0.011
	p_2/p_4	–0.2659	0.7863		
	p_3/p_4	–1.1690	0.9323		
Plateaus	p_1/p_4	3.0937	0.8399	24.81	<0.001
	p_2/p_4	0.9435	0.8687		
	p_3/p_4	0.9405	0.9095		
Terraces	p_1/p_4	3.0866	0.7088	33.95	<0.001
	p_2/p_4	1.0547	0.6877		
	p_3/p_4	0.5793	0.7535		
Lingonberry					
Crown closure	p_1/p_3	–0.0845	0.0169	26.03	<0.001
	p_2/p_3	–0.0527	0.0175		
Other berry cover	p_1/p_3	–0.0148	0.0034	22.24	<0.001
	p_2/p_3	–0.0059	0.0036		
Overstory[a]					
White spruce	p_1/p_3	–1.3268	0.4024	13.23	0.001
	p_2/p_3	–0.4738	0.3971		
White spruce – hemlock	p_1/p_3	0.3574	0.3836	14.98	0.001
	p_2/p_3	–0.7858	0.4325		
Lutz spruce	p_1/p_3	–0.5532	0.3375	13.18	0.001
	p_2/p_3	–1.3242	0.3791		
Land type association[d]					
Mountain slopes	p_1/p_3	–1.7372	0.6820	6.49	0.011
	p_2/p_3	—	—		
Hills, high relief	p_1/p_3	0.0121	0.5634	13.98	0.001
	p_2/p_3	1.4496	0.5606		
Volcanic	p_1/p_3	0.6939	0.7085	1.56	0.459
	p_2/p_3	0.9475	0.7649		
Land type[c]					
Mountain slopes	p_1/p_3	—	—	—	—
	p_2/p_3	—	—		
Forested slopes	p_1/p_3	11.4221	0.6316	327.04	<0.001
	p_2/p_3	—	—		
Nonforested slopes	p_1/p_3	3.8059	1.2411	11.38	0.003
	p_2/p_3	2.9238	1.3546		
Fans or rivers	p_1/p_3	–0.5848	0.6870	11.01	0.004

Table 3 (*concluded*).

Parameter	Value cover logit	Estimate	SE	χ^2	*P*
	p_2/p_3	–2.0183	0.6809		
Plateaus	p_1/p_3	2.0466	0.8217	12.89	0.002
	p_2/p_3	–0.0123	1.0254		
Terraces	p_1/p_3	–0.2284	0.5653	13.81	0.001
	p_2/p_3	–1.5745	0.5622		
Other berry species					
Crown closure	p_1/p_4	0.0080	0.0035	6.32	0.097
	p_2/p_4	0.0087	0.0045		
	p_3/p_4	0.0086	0.0046		
Other vegetation cover	p_1/p_4	0.0186	0.0034	32.98	<0.001
	p_2/p_4	0.0154	0.0045		
	p_3/p_4	0.0161	0.0046		
Overstory[a]					
White spruce	p_1/p_4	–0.4018	0.3024	7.84	0.050
	p_2/p_4	–0.2759	0.3978		
	p_3/p_4	0.5345	0.3940		
White spruce – hemlock	p_1/p_4	–0.0102	0.2706	4.85	0.183
	p_2/p_4	0.3281	0.3283		
	p_3/p_4	0.5881	0.3576		
Lutz spruce	p_1/p_4	–0.4060	0.2581	7.68	0.053
	p_2/p_4	–0.1909	0.3305		
	p_3/p_4	0.3838	0.3456		
Infestation[b]					
Low	p_1/p_4	0.0332	0.2346	18.16	<0.001
	p_2/p_4	0.9507	0.2834		
	p_3/p_4	0.5316	0.2884		
Medium	p_1/p_4	0.0854	0.2425	0.26	0.968
	p_2/p_4	–0.0530	0.3457		
	p_3/p_4	0.0345	0.3279		

Note: See Table 1 for definitions of cover classes (p_1–p_4).

[a]Mountain hemlock is the reference value.

[b]High is the reference value.

[c]Low- or high-relief hills is the reference value.

[d]Low-relief hills is the reference value.

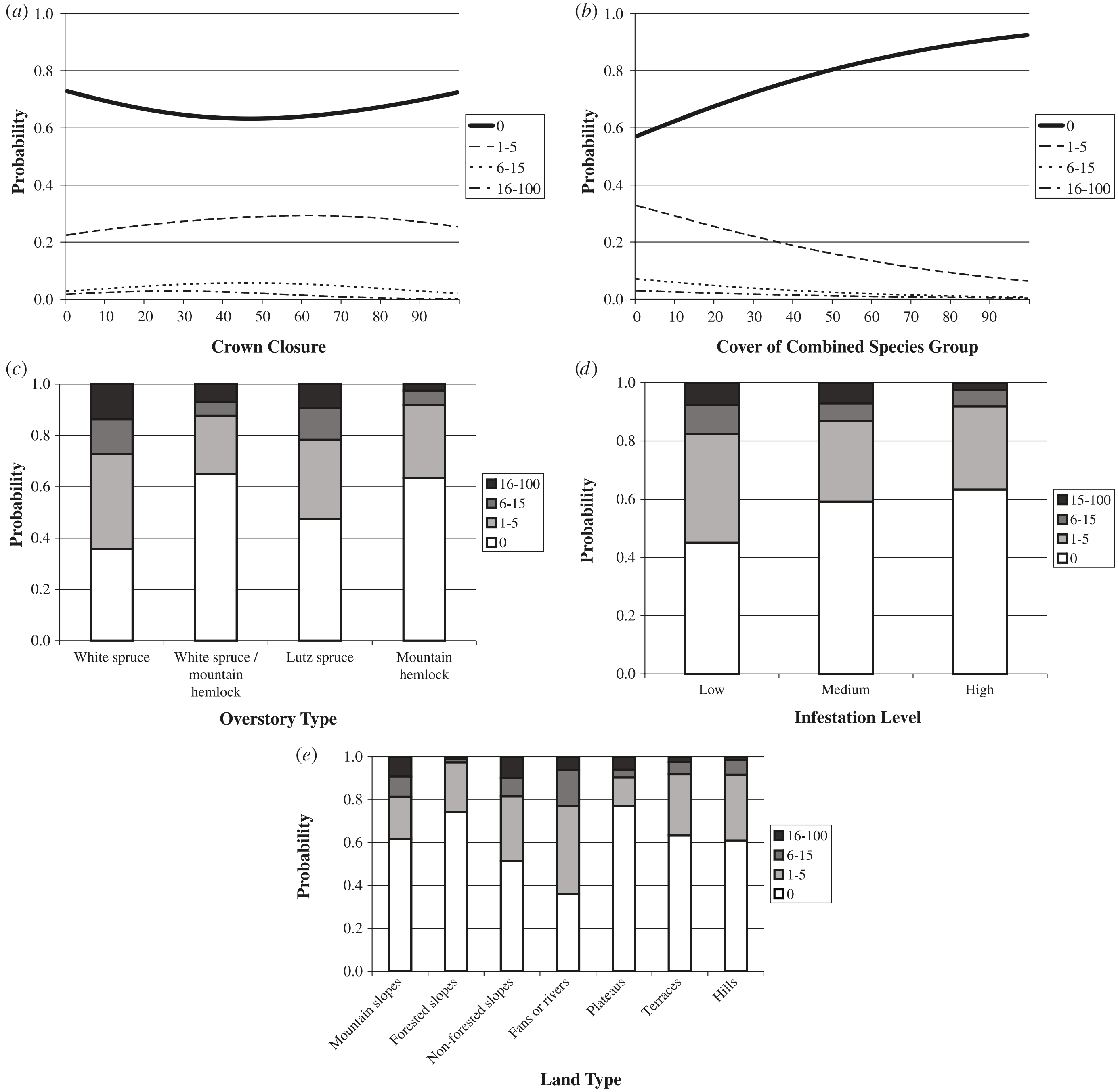
and its quadratic (crown_closure, crown_closure^2), overstory type (overstory), understory cover (either other_veg, other_-berry_cover, or other_cover); (*ii*) infestation level (infestation); and (*iii*) land type association (landassn) and land type (land type). We treated the cover variables (crown_closure, crown_closure^2, other_berry_cover, other_veg, and other_cover) as continuous variables, and we treated the remaining variables as categorical variables.

We modeled berry cover using multinomial logistic regression (Hosmer and Lemeshow 2000), which we fit via likelihood maximization using SAS PROC CATMOD (SAS Institute Inc. 1998). We used an informal forward stepwise model-building approach. First, we ran univariate regressions using each explanatory variable. Each covariate was represented by ≥4 coefficients in the multinomial logit model (e.g., the covariate land type required estimation of 18 coefficients when there were four categories of the response). Assessment of the contribution of each covariate entailed initial examination of *P* values for the corresponding set of coefficients. However, we based the decision to either retain or drop a covariate in a model on the drop-in-deviance test (Hosmer and Lemeshow 2000). We considered individual covariates significant at α = 0.10 for inclusion in subsequent models and we considered covariates in order of their preassigned weight relative to management. All initial models began with crown closure (either crown_closure alone, or crown_closure and crown_closure^2 together). We tested subsequent terms in order of their importance. If addition of a covariate, which initially appeared to be significant, yielded a nonsignificant result when added to a model, we subsequently dropped that covariate. If addition of a less important term caused a more important term already in a model to become nonsignificant, we dropped the less important term. We calculated predicted probabilities and their associated standard errors to explore the relationship between the response and each explanatory variable.

Results

We developed models for five species (bunchberry dogwood, black crowberry, false toadflax, strawberryleaf raspberry, and lingonberry) and for the combined group of other berry species (Table 3). Crown closure (either crown_closure, or crown_closure and crown_closure^2) and overstory type (three indicator variables) appeared in all six models (Figs. 1–6), and cover of the combined species group appeared in

Fig. 1. Predicted probabilities for the occurrence of each cover class obtained from the final multinomial logistic regression model for bunchberry dogwood in response to (*a*) crown closure, (*b*) cover of the other berries group, (*c*) overstory type, (*d*) spruce beetle infestation level, and (*e*) land type. For each variable, the remaining terms were held fixed at either the mean of the observed values (continuous variables) or the mode (categorical variables). The legend refers to the cover class for bunchberry dogwood.



the models developed for the five individual species. The model for the combined species group included a variable describing the cover of non-berry species in the understory. Overstory type appeared in all final models. Infestation level appeared in all models except the model for lingonberry cover. Land type association was incorporated into models for black crowberry, false toadflax, strawberryleaf raspberry, and lingonberry. Land type appeared in models for bunchberry dogwood, strawberryleaf raspberry, and lingonberry.

As crown closure increased from moderate (30%–50%) to maximum (100%) values, the probability of having low cover of berry species increased (i.e., cover of berry-producing plants and crown closure tended to be negatively associated). However, the shape of the response curve varied by species. Cover of bunchberries increased as the overstory canopy closed to about 50%, then it decreased up to 100% canopy closure (Fig. 1*a*). Black crowberry and false toadflax showed a similar response to overstory canopy with increasing cover as the canopy increased from 0% to approximately 30% then decreasing to 0 probability of occurrence as crown

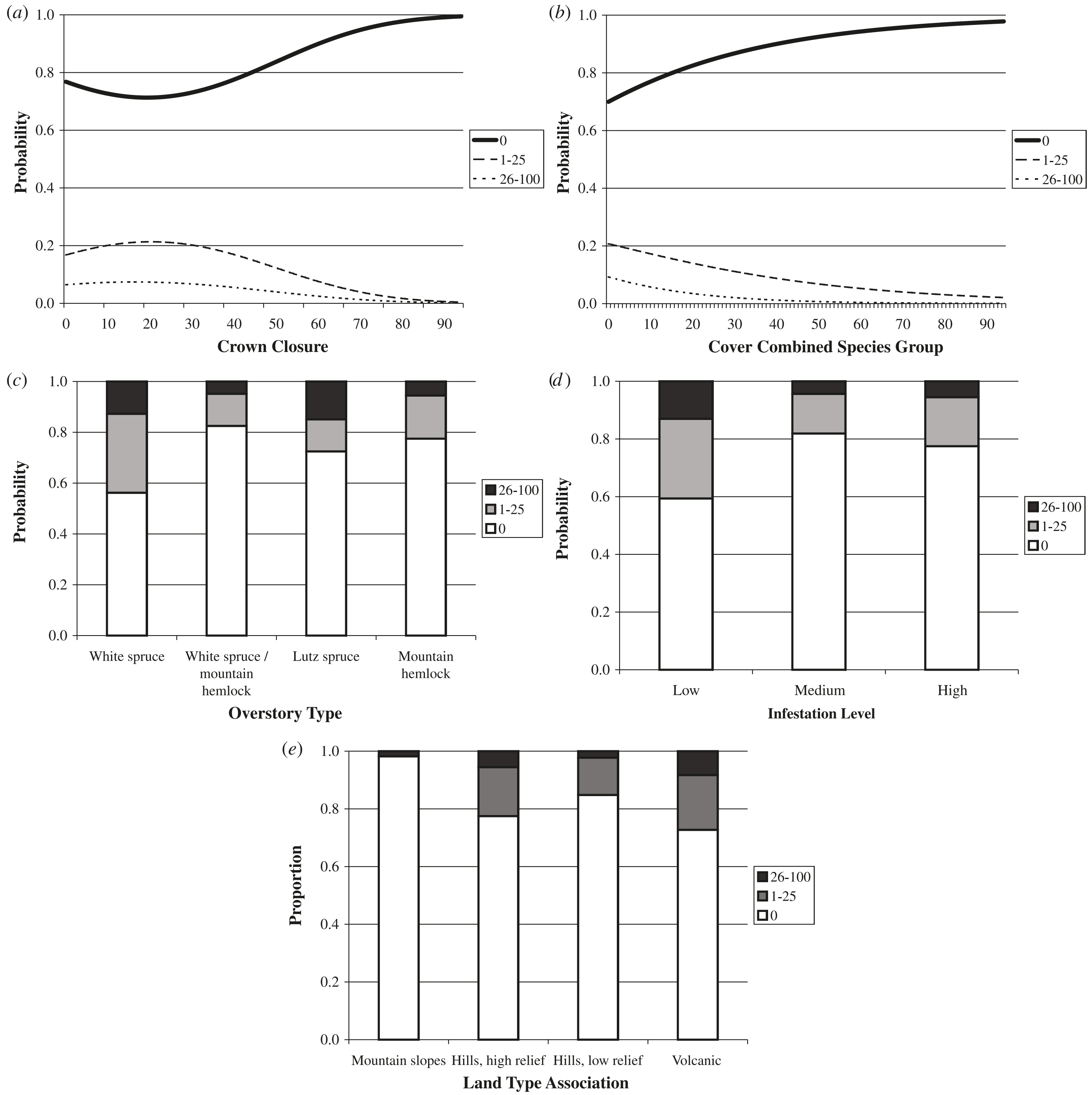
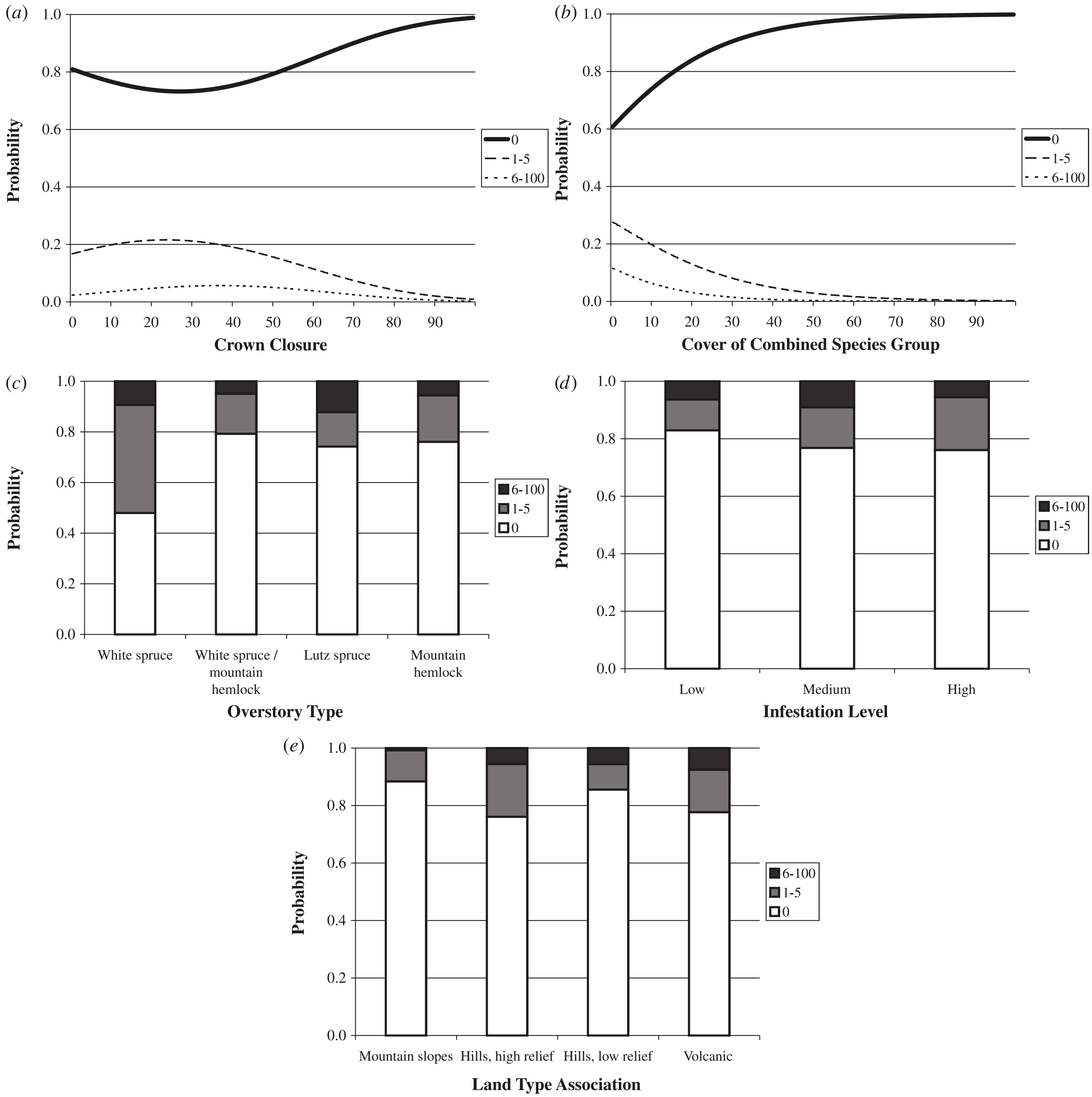


Fig. 2. Predicted probabilities for the occurrence of each cover class obtained from the final multinomial logistic regression model for black crowberry in response to (*a*) crown closure, (*b*) cover of the other berries group, (*c*) overstory type, (*d*) spruce beetle infestation level, and (*e*) land type association. For each variable, the remaining terms were held fixed at either the mean of the observed values (continuous variables) or the mode (categorical variables). The legend refers to the cover class for black crowberry.

closure approached 100% (Figs. 2*a* and 3*a*). Lingonberry cover was low to moderate as crown closure increased from 0% to approximately 50% but declined to 0 probability of occurrence as crown closure increased from 50% to 100% (Fig. 5*a*). Although the probability of moderate to high cover of all other berry species decreased as overstory canopy increased from 0% to 100%, the probability of low cover of these species remained constant, even at 100% crown closure (Fig. 6*a*). Strawberryleaf raspberry is the notable exception to this general pattern. As crown closure increased, the probability of being present, particularly in low amounts increased (Fig. 4*a*).

For bunchberry dogwood, black crowberry, false toadflax, and strawberryleaf raspberry, as cover of other berry-producing shrubs increased, the probability of having zero cover of these four species increased monotonically and the probabilities of being in the higher cover categories decreased monotonically (Figs. 1*b*, 2*b*, 3*b*, and 4*b*). Cover of lingonberry was positively associated with the combined cover of other berry species and understory vegetation

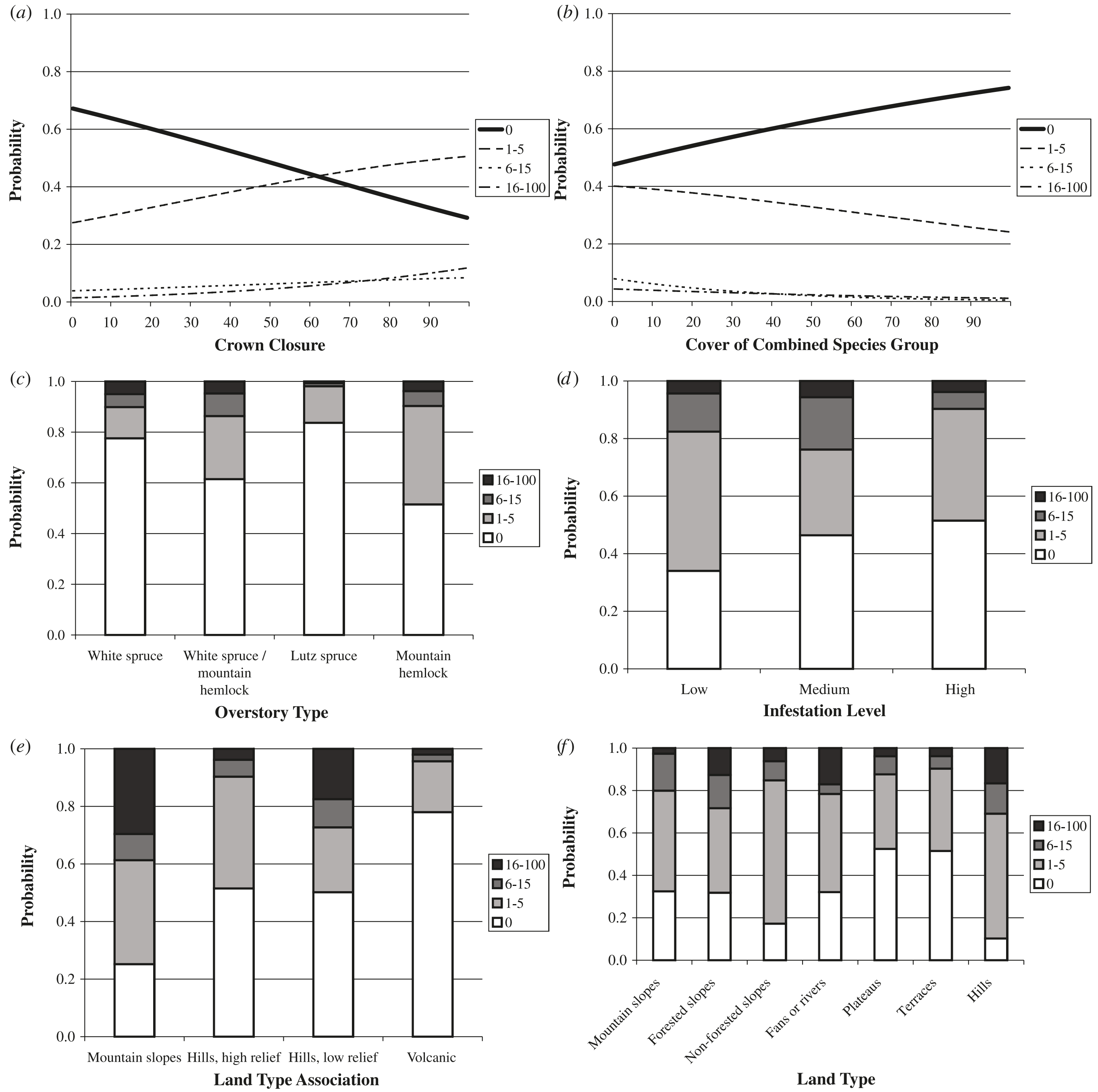
Fig. 3. Predicted probabilities for the occurrence of each cover class obtained from the final multinomial logistic regression model for false toadflax in response to (*a*) crown closure, (*b*) cover of the other berries group, (*c*) overstory type, (*d*) spruce beetle infestation level, and (*e*) land type association. For each variable, the remaining terms were held fixed at either the mean of the observed values (continuous variables) or the mode (categorical variables). The legend refers to the cover class for false toadflax.



(Fig. 5*b*). When the combined cover of other berry species was modeled, the cover of understory vegetation was included in the model (Fig. 6*a*). As the cover of non-berry species increased, the probability of being in a high cover class decreased for other berry species but the probability of being in low to moderate cover classes remained constant.

We found the highest probability of cover of bunchberry dogwood, black crowberry, false toadflax, and lingonberry present in the white spruce overstory type (Figs. 1*c*, 2*c*, 3*c*, and 5*c*). Bunchberry dogwood, black crowberry, and false toadflax had a corresponding high probability of zero to low cover in the white spruce – mountain hemlock and mountain hemlock overstory types (Figs. 1*c*, 2*c*, and 3*c*). Bunchberry dogwood also showed a moderate probability of low to high cover being present in the Lutz spruce overstory type (Fig. 1*c*). Strawberryleaf raspberry was more closely associated with forests with a mountain hemlock overstory than a white or Lutz spruce overstory (Fig. 4*c*). The other berries group showed a similar response to all overstory types (Fig. 6*c*).

Fig. 4. Predicted probabilities for the occurrence of each cover class obtained from the final multinomial logistic regression model for strawberryleaf raspberry in response to (*a*) crown closure, (*b*) cover of the other berries group, (*c*) overstory type, (*d*) spruce beetle infestation level, (*e*) land type association, and (*f*) land type. For each variable, the remaining terms were held fixed at either the mean of the observed values (continuous variables) or the mode (categorical variables). The legend refers to the cover class for strawberryleaf raspberry.

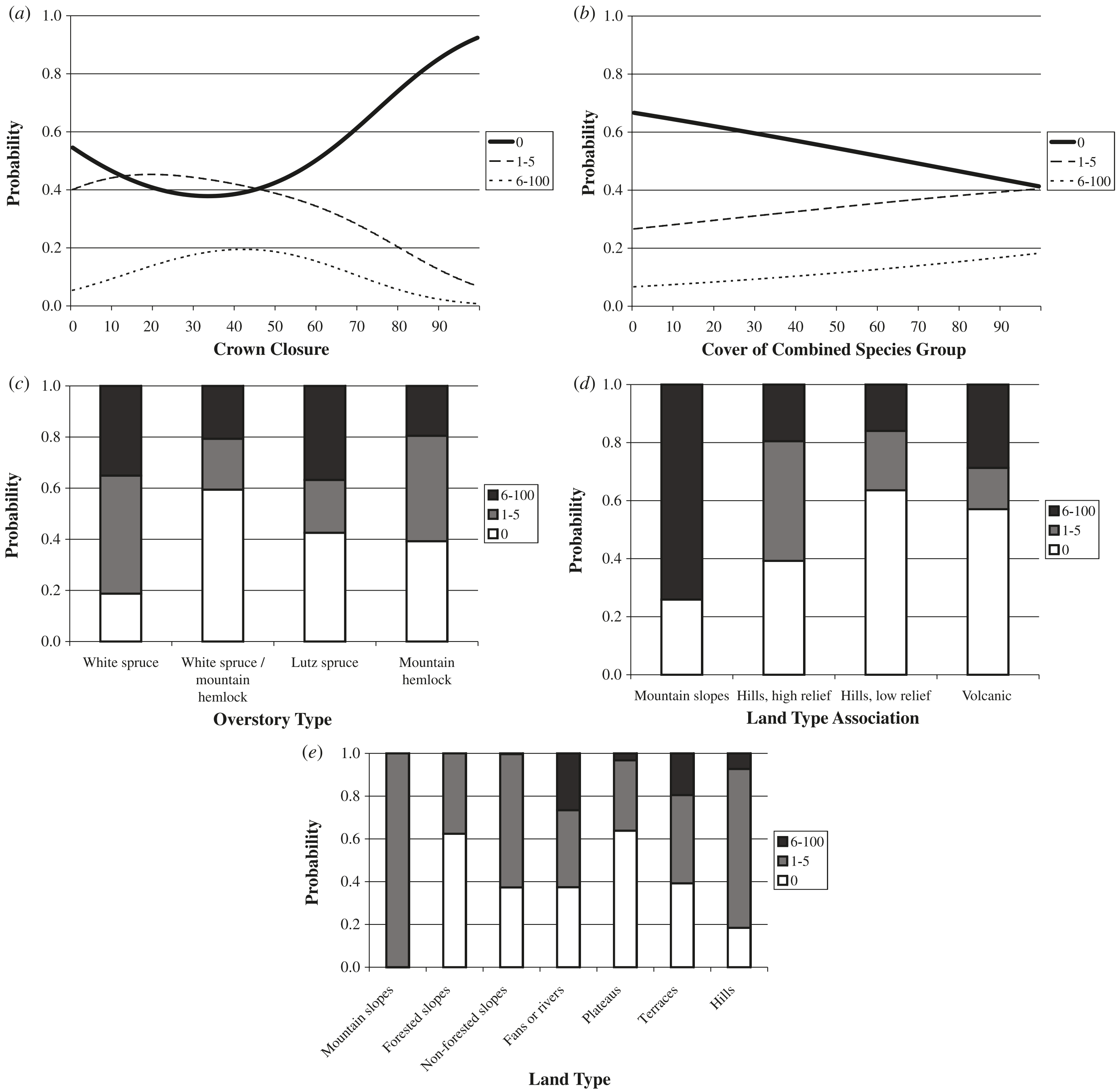


Although the level of spruce beetle infestation had an apparent effect on the cover of some of the berry species evaluated, the effect did not appear to be large. Generally, the probability of having zero cover was either greatest at medium infestation (Figs. 2*d* and 6*d*) or at high infestation (Figs. 1*d* and 4*d*), suggesting that these species (bunchberry dogwood, black crowberry, strawberryleaf raspberry, and other berry species) occurred less frequently in forests with medium to high infestation. Cover of these species may have decreased as a result of other factors associated with high levels of infestation and may not have responded directly to level of infestation. Responses by berry species to land type association and land type did not show consistent patterns across species (Figs. 1*e*, 2*e*, 3*e*, 4*e*, 4*f*, 5*e*, and 5*f*).

Discussion

Ecosystem management involves the integration of ecological, economic, and social objectives. The ecological objectives often include conservation of biological diversity

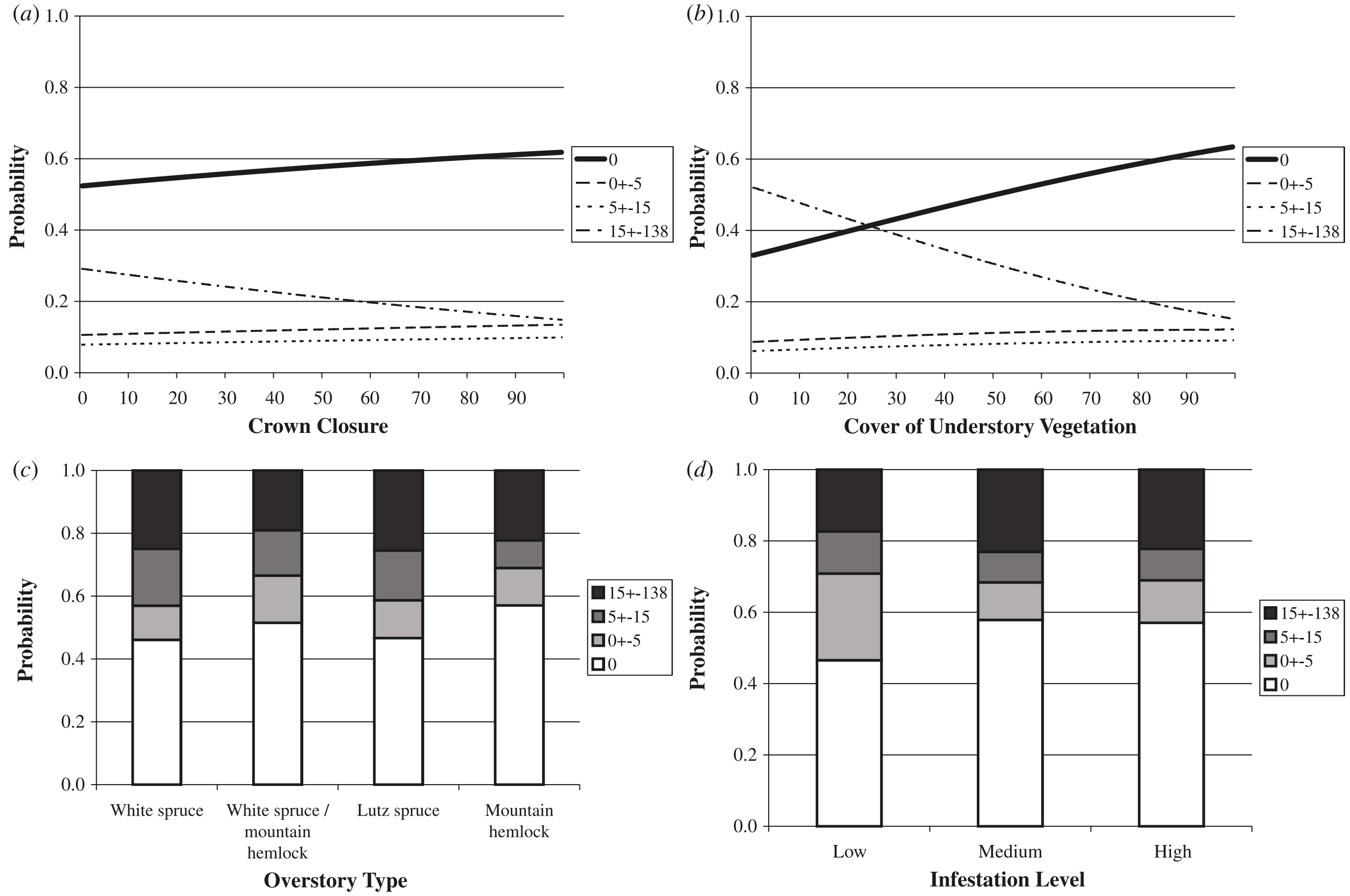
Fig. 5. Predicted probabilities for the occurrence of each cover class obtained from the final multinomial logistic regression model for lingonberry in response to (*a*) crown closure, (*b*) cover of the other berries group, (*c*) overstory type, (*d*) land type association, and (*e*) land type. For each variable, the remaining terms were held fixed at either the mean of the observed values (continuous variables) or the mode (categorical variables). The legend refers to the cover class for lingonberry.



and ecosystem integrity. Management plans should address these ecological objectives while also allowing economic and social uses of the landscape. Successful management will ensure ecological sustainability of the landscape (i.e., goods and services are provided while biological diversity and ecosystem integrity are maintained). Although berry-producing plants may be a minor component of the ecological system, they fill important functions that include contribution to biological diversity, forage for wildlife, human subsistence food, commercial products, and recreation opportunities. Management that addresses the ecological relationships of berry-producing species will help to ensure ecological sustainability and will continue to meet the needs of the users of this resource. Not adequately considering these relationships will likely result in reductions in berry productivity with consequences to wildlife and people.

American black bears on the Kenai Peninsula use berries and other plant material as their primary food source because they are precluded from using the abundant salmon (*Oncorhynchus* spp.) resource by brown bears (Fortin et al.

Fig. 6. Predicted probabilities for the occurrence of each cover class obtained from the final multinomial logistic regression model for the other berries group in response to (*a*) crown closure, (*b*) cover of understory vegetation, (*c*) overstory type, and (*d*) spruce beetle infestation level. For each variable, the remaining terms were held fixed at either the mean of the observed values (continuous variables) or the mode (categorical variables). The legend refers to the cover class for the other berries group.



2007). Persistent berries also provide a critical food source for migrating birds in the fall and spring and for resident birds and small mammals throughout the year (Table 4). Migration may constitute the most vulnerable and unpredictable period of the annual cycle for birds (Sillett and Holmes 2002), suggesting the critical nature of the conservation of migratory stopover habitat, including food sources like berries (Mehlman et al. 2005).

Alaskans have a long cultural tradition of subsistence use of wild berries. They were very important to Alaska Natives and to early European settlers, and are still an important part of many people's diets (Table 4) (Alaska Magazine 1982; Pojar and MacKinnon 1994). Wild berry products are also a significant source of income to many people especially in south-central and central Alaska (Pilz et al. 2006). Although berry production varies each year, using ecological information to manage the landscape to enhance production of berry-producing species will facilitate berry crops adequate to support the needs of wildlife and people.

Previous work indicated that berry productivity by black crowberry, false toadflax, and the other berries group on the eastern Kenai Peninsula generally increased with increasing levels of white and Lutz spruce mortality from spruce beetles, presumably because of the release of berry-producing plants from competition with overstory white or Lutz spruce for light, nutrients, and water (Suring et al. 2006). However, tests of this hypothesis are lacking (Wender et al. 2004). Whereas predicted probabilities of the occurrence of false toadflax cover followed a similar pattern in this analysis, we found the greatest predicted probabilities for the occurrence of cover of bunchberry dogwood, black crowberry, strawberryleaf raspberry, and the other berries group at low infestation levels. These findings indicate that higher levels of crown closure typically associated with low infestation levels resulted in higher cover of berry-producing plants but lower berry production; whereas high infestation levels resulting in reduced crown closure supported lower cover of berry-producing plants but greater productivity of berries. This is supported in the literature, in that Pakonen et al. (1988) reported an increase in vegetative growth in whortleberry (*Vaccinium myrtillus*) plants that did not produce berries. Additionally Tolvanen and Laine (1997) observed that reproduction reduced vegetative growth in lingonberries. Bunnell (1990) also reported that berry production in salal (*Gaultheria shallon*) only occurred at ≤33% canopy closure, while vegetative growth and reproduction occurred under very sparse and dense closure.

Throughout south-central Alaska, management activities have increased in response to massive infestations of spruce beetles (Berg et al. 2006; Goodman and Hungate 2006). Re-

Table 4. Ecological relationships, uses, and response to landscape management of common berry-producing species on the Kenai Peninsula, Alaska.

Species	Ecological relationships	Uses	Response to management	References
Bunchberry dogwood	Common in 55- to 90-year-old thinned white spruce stands, most common plant in south-central Alaska, occurring on 1059 of 2293 locations, peaked in abundance in the tall shrub-sapling stage (3–30 years) of white spruce forests, decreased as trees became dense (26–45 years), then increased in association with hardwoods (45–150 years), and remained constant or decreased slightly into the old white spruce stage (150–300 years)	Savannah sparrows (*Passerculus sandwichensis*), American robins (*Turdus migratorius*), spruce grouse (*Falcipennis canadensis*), and northern red-backed voles used fruit and (or) buds; subsistence harvest	Maintain white spruce overstory crown closure at 50%	Martin et al. 1951; Foote 1983; Dyrness et al. 1986; Burger 1987; Jones 1990; DeVelice et al. 1999; Pilz et al. 2006
Black crowberry	Fruit matures from August to late fall and persists through the winter under snow cover	Black bears, northern red-backed voles, and birds forage on fruits throughout the year; subsistence harvest	Maintain white spruce overstory crown closure at 10%–40%	Martin et al. 1951; Viereck and Little 1972; West 1982; MacHutchon 1989; Norment and Fuller 1997; Pilz et al. 2006
False toadflax	Most abundant in open white spruce stands >250 years old, also found in open and closed, mature white spruce and black spruce forests 70–>180 years old	Spruce grouse and northern red-backed voles eat the berries	Maintain white spruce overstory crown closure at 10%–40%	Ellison 1966; Neiland and Viereck 1977; Dyrness and Grigal 1979; West 1982; Reynolds 1990; Viereck et al. 1993
Strawberryleaf raspberry	Second most common plant in south-central Alaska, occurring on 917 of 2293 locations, decreased after burning	None reported	Cover will increase with increased crown closure in white spruce – mountain hemlock and mountain hemlock overstory types	DeVelice et al. 1999; Boucher 2003
Lingonberry	Plants growing under a closed canopy rarely produce fruit or flowers, plants growing under an open canopy commonly produced fruit, biomass increased with decreased crown closure	Food source during winter (e.g., northern red-backed voles, black bears) and spring migration (birds); subsistence harvest; commercial harvest; recreation harvest	Light to moderate disturbance (e.g., fire, timber harvest) to keep crown closure in white spruce overstory type from 10% to 50%	Hatler 1972; Oldemeyer and Seemel 1976; Lehmushovi 1977;Hall and Shay 1981; West 1982; Engelmark 1987; Dyrness et al. 1988; Kuchko 1988; Norment and Fuller 1997; Ihalainen et al. 2003; Pilz et al. 2006; Suring et al. 2006

source managers may use these and other results (Suring et al. 2006) to address growth and production of berry-producing plants in association with other ecosystem services and values in boreal forests. Information on the growth of berry-producing plants may be incorporated into descriptions of desired future conditions (e.g., landscape characteristics, overstory tree species, crown closure) to establish management objectives that include berry species (Meyer and Swank 1996). Information on the response of berry-producing species relative to disturbance activities (e.g., insect infestation, fire, timber harvest) may then be incorporated into the development of management prescriptions designed to achieve desired future conditions.

Conclusions

We showed how berry-producing species responded with environmental variables on the Kenai Peninsula, Alaska. Our findings indicate that berry cover did vary by forest overstory type and by ecological conditions. White and Lutz spruce forests may be managed to enhance berry cover, although response of some species may vary by land type and land type association. Use of different management techniques (e.g., timber harvest, prescribed fire) to manipulate crown closure and subsequently berry cover may result in different outcomes (Suring et al. 2006). Consideration of these findings in the development of strategies to manage forests in this area provides opportunities to craft and meet multiple objectives.

Acknowledgments

The USDA Forest Service, Chugach National Forest, provided funding for this project. The encouragement and support of M. Novy and S. Zemke made this study possible. T. McDonald, Western EcoSystems Technology, Inc. assisted with study design and initial data analysis. A. Poe and B. Brown assisted with data synthesis. C. Madsen developed and implemented the process for converting digital photographs to measurements of crown closure. K. Preston assisted with aspects of study design and data processing that incorporated geographic information system analyses. This study could not have been completed without the dedication and hard work of numerous biological technicians and volunteers. We thank each of you.

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