Aspen Community Restoration Project
Summary of Avian Monitoring – 2002-2016

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INTRODUCTION

The importance of quaking aspen (*Populus tremuloides*) to birds and other wildlife in western North America has long been appreciated by biologists (Salt 1957, Flack 1976, DeByle 1985). Recent studies from the Sierra Nevada, and the Lake Tahoe Basin in particular, have demonstrated that aspen habitats typically support much greater diversity, richness, and abundance of birds than adjacent habitats (Heath and Ballard 2003, Richardson and Heath 2004), and several bird species have shown a strong affinity with aspen, including Northern Goshawk (*Accipiter gentilis*), Red-breasted Sapsucker (*Sphyrapicus ruber*), Dusky Flycatcher (*Empidonax oberholseri*), Warbling Vireo (*Vireo gilvus*), Swainson's Thrush (*Catharus ustulatus*), and MacGillivray's Warbler (*Oporornis tolmiei*) (Finch and Reynolds 1988, Richardson and Heath 2004). Swainson's Thrush (Stefani 1998) and Warbling Vireo (Gardali et al. 2000, Gardali and Jaramillo 2001), in particular, are two species notable for significant population declines in the Sierra Nevada or western North America, making their association with degraded and declining Sierra aspen habitats of great conservation interest.

The apparent benefits to birds breeding in aspen stands are many. Ground-nesting birds benefit from an exceedingly thick and diverse herbaceous layer and deep leaf litter (Kuhn et al. 2011), which aids in potential for nest concealment (Flack 1976, DeByle 1985). Both primary and secondary cavity nesters benefit from aspen's susceptibility to heart rot and an associated abundance of cavity-bearing trees (DeByle 1985, Daily et al. 1993). It is highly likely that one of the main benefits to all birds breeding in aspen stands is the increased abundance and diversity of invertebrate prey (Winternitz 1980), and aspen trees and stands may provide refugia from conifer-associated nest predators, such as Steller's Jay (*Cyanocitta stelleri*) and Douglas' Squirrel (*Tamiasciurus douglasii*; Richardson 2007, Richardson and VanderWall 2007).

Due to these and many other ecological benefits, aspen were identified in the Lake Tahoe Watershed Assessment (Murphy and Knopp 2000) as Ecologically Significant Areas (ESAs), yet aspen occupy less than two percent of the landscape on the Lake Tahoe Basin Management Unit. Further, many of these remaining habitats have become degraded, and more may disappear for wildlife in the foreseeable future. Because western aspen primarily reproduce through vegetative suckering, generally following a disturbance of some kind, whole stands can succumb to conifer succession within a few hundred years if no disturbance occurs (e.g., fire suppression). Much of the aspen in the Lake Tahoe Basin is threatened in this manner (Shepperd et al. 2006).

The Aspen Community Restoration project aims to move aspen stands determined to be at Moderate, High, or Higher risk of loss from the landscape on Forest System lands within the Lake Tahoe Basin, toward the desired condition where 1) the upper canopy is dominated by aspen; 2) conifers compose less than 25% of the canopy; and 3) aspen regeneration is vigorous. Possible treatments primarily include conifer removal to reduce or eliminate conifer encroachment, but may also include aspen removal to promote root stimulation and stand regeneration, aspen root separation, or prescribed fire. In 2009-2010, we implemented a monitoring program to establish baseline and control data of the bird community in these stands, monitor the effects of the treatments on the bird community, and help better inform future decision-making processes regarding aspen stand management in the Lake Tahoe Basin. Here we incorporate control data from 2002-4 and 2008 and summarize results from the 2009, 2010, 2012, and 2016 field seasons.

METHODS

Study Area and Bird Sampling

Study sites were located within seven clusters of aspen stands, portions of which were previously treated (2004) or slated for treatment in recent years (2009-2013), and two clusters of stands to serve strictly as control for year effects (Figures 1-7). We conducted 5-min, 50 m, fixed-radius point counts at 58 independent stations following the guidelines of Ralph et al. (1993, 1995). Two clusters of stations, comprising 14 stations, were sampled in 2002, 2003, and 2004 as part of an earlier study (Richardson and Heath 2004); one cluster, comprising 10 stations, was sampled in 2008 as part of an earlier study (Richardson 2010); seven clusters, comprising 54 stations, were sampled in 2009; five clusters, comprising 35 stations, were sampled in 2010; five clusters, comprising 38 stations were sampled in 2012, and seven clusters, comprising 52 stations were sampled in 2016 (Table 1). The decrease in sampling effort from 2009 to 2010 and 2012 was due to funding constraints. As much as possible, stations were placed at least 200 m apart to avoid double counting of territorial birds and to ensure independence of stations. Many stands were quite small, thus we attempted to place stations in the very center of the largest areas of aspen available, to maximize the signal of any “aspen effects” for pre-treatment years, and treatment effects in post-treatment years. Treatments in the Tahoe basin have principally comprised manual conifer-thinning and piling up slash for burn piles. Blackwood canyon treatments involved heavy logging equipment, and were much more aggressive in the amount of conifer material they removed. Portions of the Ward Canyon treatment slash piles were burned prior to sampling in 2012, and one treatment and slash pile burn happened between sampling in 2012 and 2016; slash piles at Taylor/Tallac Creek, Cold Creek, and Secret Harbor Creek sites were burned in the fall of 2012, after bird sampling was completed for the year. Three of the Secret Harbor Creek stations contained no aspen of any size class. We recorded all birds observed, as well as Douglas’ Squirrel, and type of detection (song, call, or visual), and denoted whether the individual was within or outside of the 50 m radius census plot. All stations were sampled three times during the peak songbird breeding season (24 May-3 July in 2009; 1 June-9 July in 2010; 6 June-10 July in 2012; 25 May-6 July in 2016). Pre-treatment data for the Secret Harbor Creek site were collected as part of a different study between 1 June and 4 July 2008. Visits to individual stations were spaced at least 7 days apart.

Habitat Assessments

Vegetation data were collected following completion of the last round of point counts (54 stations in 2009; 10 stations in 2010: 4 new stations, 6 post-treatment reassessments; 22 post-treatment reassessments in 2012; 1 reassessment due to beaver-activity (Figure 8) and 23 post-treatment reassessments in 2016). Our habitat estimates followed a modified version of the relevé technique (Ralph et al. 1993). In short, for a 50 m radius plot, centered on each point count station, we estimated percent herbaceous ground cover, as well as percentage cover for every species of woody plant for each of two height categories: "shrub" (0.5 - 5 m) and "tree" (>5 m). Overall canopy cover was measured by averaging four readings with a spherical densiometer, one reading in each cardinal direction. Of the dozens of potential vegetation and environmental variables available, we selected eight that we felt would best contribute to models predicting bird species richness, mean bird abundance, and Warbling Vireo, Steller's Jay, and Douglas' squirrel abundances within these stands (Table 2). These variables have proven to be reliable predictors of these indices in past research, particularly in aspen stands (Richardson 2007, Richardson 2010, Richardson and Heath 2004). While these estimates may be somewhat subject to bias, all habitat assessments have been made by the same observer. Thus, any observer bias is consistent across sites.

Data Analysis

We calculated total bird species richness (BSR) and mean bird abundance (MBA) for each station, restricting our data set to detections ≤ 50 m and further limiting the indices to include species most reliably sampled with the point count method. We therefore removed nocturnal species (e.g., *Strigidae*) and species with territories typically too large to ensure independence of individual point count stations (e.g., *Anseriformes*, *Corvus corax*). A complete list of common and Latin names for all species used in analysis is presented in the Table 3.

Our main interest in these analyses was to investigate any potential ill effects of treatments in the short-term immediately following treatments and anticipated ongoing post-treatment positive effects. By 2016, however, we had enough years sampled to investigate year effects in our models. In our report summarizing 2012 results (Richardson 2012), we investigated treatment effects by plotting the reduction in percent absolute conifer cover from pre- to post-treatment vegetation assessments, against the change in bird indices averaged from pre- and post-treatment years. By 2016, we had data available spanning 2-12 years after conifer-thinning treatments, and therefore built separate models to specifically look at both reduction of conifer cover and Years Post Treatment (YPT) as a variables within treated plots.

We looked for highly correlated predictor variables when building full models in an attempt to reduce dimensionality, and typically found sufficient multicollinearity to warrant exclusion of absolute tree cover from the full model, as this predictor consistently demonstrated a strong linear relationship with absolute tree-class conifer cover, tree-class aspen cover, or both. Optimal general linear regression models were selected based on lowest Akaike's information criterion (AIC) score, using the Step function, as implemented in Program R, 2.4.1 (R Development Core Team 2006). Predictor variables retained in models within 4.00 ΔAIC from the best model are presented in the results and can be considered as have explanatory value in competitive models. All statistical tests were performed using Program R, 2.4.1 (R Development Core Team 2006). Model and parameter significance was designated at $P < 0.05$.

RESULTS AND DISCUSSION

Across the 68 point count stations sampled over this study, we detected 74 species. Seventy-one of these species were detected ≤ 50 m from point count stations, and 62 of these were deemed suitable for inclusion in analyses (see METHODS: Data Analysis). Of these 62 species, only 11 were observed at ≥ 50% of all sites, despite sampling across eight seasons. This statistic speaks to both the high diversity of birds encountered at these sites, as well as the diversity of broader environmental contexts within which these sites were situated. These 11 species were Western Wood-Pewee, Warbling Vireo, Steller's Jay, Mountain Chickadee, American Robin, Nashville Warbler, Audubon's Warbler, MacGillivray's Warbler, Wilson's Warbler, Western Tanager, and Oregon Junco. Figures 9-12 show total detections and number of stations detected for the 16 most commonly detected and abundant bird species in each respective year from 2009-2016.

In 2009, average MBA for the 54 count stations (averaged across the three sampling periods) was 6.84 (± 0.38 SE) individuals and ranged from 2.33-15.33 individuals. In 2010, average MBA for the 35 count stations was similar, at 8.10 (± 0.39 SE; range = 4.33-14.00) individual birds. In 2012, average MBA continued to nudge slightly higher, at 8.54 (± 0.49 SE; range = 1.67-14.67) individual birds. In 2016 MBA for the 52 stations sampled that year was 7.99 (± 0.26; range 0.67-21.33). Many of the lowest counts through the entire study period were found along the Cold Creek transect (Table 4), and likely reflected the extremely narrow extent of the aspen stringer, bordered by a sparse East Side Pine community with little to no understory, and perhaps a bit of creek noise hampering detection. The very lowest counts were the few Secret Harbor Creek stations with no aspen cover at all. The highest counts were widely spread among count stations located in the most pure, extensive, and mature aspen stands (e.g. a few stations found at Logan House Creek and Fountain Place). In the overall 2002-2016 analysis, parameters included in models ≤ 4.00Δ AIC from the best model were tree-class conifer, shrub-class aspen, and herbaceous understory. This was very similar to the narrow subset of results examined in Richardson (2012), minus tree-class aspen and shrub cover. Important to note, absolute percentage of tree-class conifer was negatively correlated with MBA (Table 6a). Percent cover of shrub-class aspen and herbaceous ground cover were significantly positively correlated with bird abundance (Table 6a). Shrub-class aspen is particularly notable in that it may represent a proxy for the more general aspen regeneration and rebound that some of these sites experienced 2-5 growing years after conifer removal (Figures 13, 15a), most experienced strongly 6-12 years after conifer removal (Figure 14), or even ongoing recovery from the removal of grazing pressures in the case of a few Taylor/Tallac Creek stations (Figure 15b).

In 2009, average BSR for the count stations (totaled over the three sampling periods) was 11.41 (± 0.49 SE) species and ranged from 5–22 species. In 2010, average BSR was 12.09 (± 0.43 SE; range = 7-16) species, and in 2012, average BSR was 12.24 (± 0.62 SE; range = 4-20). In 2016, overall average BSR was 11.36 (± 0.27; range = 1-22). Again, low species richness was most consistently found along the Cold Creek transect

(Table 5) or in those Secret Harbor Creek stations with no aspen, but high species richness was distributed even more broadly across transects. Parameters included in models ≤ 4.00 ΔAIC from the optimal model were tree-class conifers, shrub cover, and herbaceous cover. Conifer cover was again included in the best-fit model (Table 6b), and was also negatively correlated with BSR. Herbaceous ground cover and shrubs were also retained in the optimal model, and were significantly positively correlated with BSR in the case of herbaceous understory.

Conforming with the smaller subset of analyses from Richardson (2012), in the full 2002-2016 analyses both community indices demonstrated stronger negative correlations to coniferous cover than positive correlations to aspen cover, suggesting that the density or extent of conifers within these aspen stands maybe a more important habitat criterion for these birds than the density or extent of aspen themselves. This may also be an issue of scale, as both bird indices and vegetation assessments in these models are fixed to a 50m radius. We predicted in 2010 that, if the birds are responding (negatively) primarily to dense conifers, then removal of the conifers might produce a rapid response. Whereas, if birds are responding primarily to the coverage of aspen, significant treatment effects may not become apparent until new generations of aspen suckers have had a chance to mature, a process that may take many years.

One of the great concerns of severe habitat modifications is that the short-term effects may be detrimental to the very wildlife one is trying to improve habitat for. Of particular concern was the possibility that the mechanical thinning at Blackwood Canyon might cause too much disturbance, and leave too little canopy, for the bird communities to quickly rebound from the aggressive treatment. This was definitely not the case, and we were relieved to find that all of the post-treatment sites demonstrated a high volume of bird activity during our first round (and also subsequent rounds) of surveys. Indeed, in 2012 it appeared that some of the treated sites might actually have more bird activity than they had in previous, pre-treatment years, and this trend continued into 2016. This might seem surprising for a site like Blackwood, where there was almost zero understory and mid-canopy trees left behind, but the simple fact of those sites is that prior to treatment they were too choked with dense conifers to support much of a bird community in the first place. Opening up the forest gave the birds access to the aspen and the rest of the canopy in a way that they probably had a difficult time exploiting prior to treatment.

We attempted to investigate treatment effects and, more specifically the effect of time since treatment, in the habitat models, but with only 26 treated stations we lacked sufficient sample size to confidently look for treatment effects amidst the noise of so many other habitat variables. Nevertheless, controlling only for decrease in percent conifer cover and year, and ignoring all other variables, both Mean Bird Abundance and Bird Species Richness demonstrated an increasing trend with treatment, but neither was significant. With p-values of 0.059 and 0.154, respectively, this is likely a power issue. We felt it also was worthwhile to explore the data for any trends in relation to how many conifers were removed in the treatments (Figures 16, 17). These relationships conformed to our expectations in 2012, however we did not expect to see a noticeable response only 1-2 growing seasons post-treatment (Richardson 2012). Similarly weak, but consistently trending relationships persisted into 2016 when bird indices again demonstrated an increase correlated to the decrease in percent tree-class conifer cover again (Figure 16). The important thing to note here is that almost all of the changes in the indices were positive, a desired outcome. Relationships were understandably even weaker for abundances of individual species, although they did trend in the predicted direction, with Warbling Vireos increasing, and Steller's Jays decreasing, after conifer removal (Figure 17).

The strong correlation of the two bird indices with herbaceous understory is consistent with other recent work in the region (Richardson and Heath 2004). It is unclear whether herbaceous cover provides direct benefits to aspen-breeding birds or if it is merely associated with hidden factors that we failed to measure or parameterize (e.g., moisture, abundance of invertebrates). At these sites, it was often associated with a high percentage of aspen in the canopy and negatively correlated with a coniferous overstory and thick coniferous encroachment. The herbaceous community experiences significant decreases in species richness and diversity with succession to conifer in the canopy (Harper 1973, Korb and Ranker 2001, Kuhn et al. 2011), and Harper (1973) found that understory production decreased by 50% where the canopy was composed of a high percentage of conifers (>50%). At many of the stands treated, release from conifer encroachment through thinning or natural disturbance will likely stimulate herbaceous growth by increasing both available moisture and sunlight needed by these plants. Thus far, the increase in herbaceous understory has appeared to be somewhat slow to recover at treated sites, but there has been a noticeable and quantifiable increase at a few of the stations. This process of release can be seen readily in other communities within the Lake Tahoe Basin, as well (e.g. within the footprint of the Angora Burn). If the increased herbaceous cover provides direct benefits to the birds, then we can predict increases in both MBA and BSR in heavily encroached stands, following conifer removal as part of the Aspen Community Restoration Project.

Warbling Vireo was the most numerous species observed during counts in the four principal years of the study (Figures 9-12), plus the 2002-2004 sampling that was focused on aspen (Richardson and Heath 2004). Further, they were nearly ubiquitous, occurring at 48 (88.9%) of the 54 sampling stations in 2009, 30 (85.7%) of the 35 sampling stations in 2010, 29 (76.3%) of the 38 stations in 2012, and 47 (92.0%) of the 52 sampling stations in 2016. Their distribution was not uniform, however, and parameters included in models of Warbling Vireo abundance $\leq 4.00\ \Delta AIC$ from the top model, were tree-class aspen and shrub cover. In the optimal model, both shrubs and tree-class aspen were positively correlated with Warbling Vireo abundance, tree-class aspen strongly so (Table 6c). This species' apparent preference for high density, mature stands is consistent with other, recent work from the region (Richardson and Heath 2004). By promoting larger, more pure aspen stands, the Aspen Community Restoration Project should, over time, provide ideal habitat for high densities of Warbling Vireos and other aspen-associated species. Indeed, 2016 saw the highest average numbers of Warbling Vireos of the study to date (1.42 per count at stations where encountered).

Douglas' Squirrels were recorded at 35 (64.8%), and Steller's Jays at 27 (50%), of the 54 sampling stations in 2009. In 2010, Douglas' Squirrels were recorded at 27 (77%), and Steller's Jays at 25 (71%), of the 35 sampling stations. In 2012, Douglas' Squirrels were recorded at 30 (78.9%), and Steller's Jays at 20 (52.6%), of the 38 sampling stations. In 2016, Douglas' Squirrels were recorded at 26 (52%), and Steller's Jays at 16 (30.8%) of the 52 sampling stations. The apparent upward shifts in the middle years is surely a reflection of not sampling the Fountain Place and Logan House Creek clusters in 2010 and 2012, but again in 2016. These are clusters that had very few detections of either species in 2009 and 2016. Not surprisingly, abundances of the two conifer-associated species were both negatively correlated with tree-class aspen cover, and squirrels were positively correlated with tree-class conifer cover (Table 6d,e). Among models of jay abundance ≤ 4.00 ΔAIC from the best-fit model, Steller's Jays were also positively correlated with shrub-class willow cover and total canopy cover. Through the removal of conifers in high-risk stands, the Aspen Community Restoration Project will not only help protect the long-term viability of the aspen trees, it is predicted to help reduce the number of conifer-associated that affect nest success among aspen-breeding birds (Figure 18, Richardson 2007).

All of the evidence thus far strongly suggests that the Aspen Community Restoration Project is succeeding in promoting not only aspen stand health and regeneration, but also avian species richness and abundance. We predict that these changes will continue in a positive trajectory until conifer recruitment again begins to place heavy competition with these aspen, a condition that may occur within a surprisingly short time interval (Berrill et al. 2016). In the meantime, we recommend continuing aggressive conifer thinning treatments on as many aspen stands as funding and opportunity allows. Based on the positive wildlife response we witnessed in Blackwood Canyon, and the simple fact that removing as many parent conifers as possible will reduce the potential for recruitment of new trees, we also recommend that treatments be as aggressive as possible (e.g. mechanical thinning, removing larger diameter trees, etc.), particularly where large, mature aspen stands are threatened. Treating large, decadent stands will likely have a larger, longer-lasting impact, and such treatments also benefit from the economies of scale (Berrill et al. 2016, Berril et al. 2017). A few candidate stands that we recommend for treatment include pockets in Ward Canyon that were skipped over (including the stand at Point Count Station 08), portions of Cold Creek that were not treated, and several stands in the Incline Creek drainage.

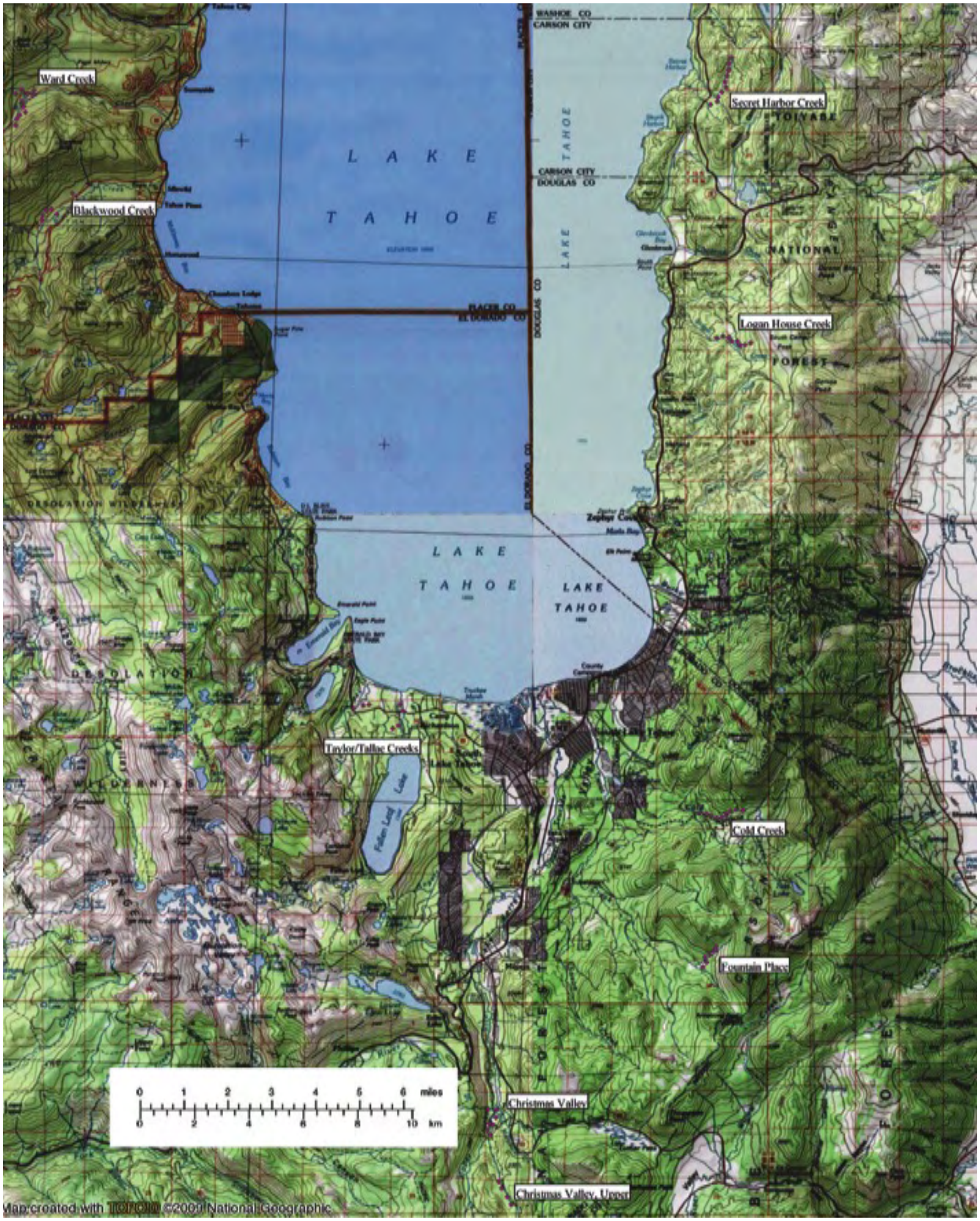


Figure 1. Overview map depicting locations of clusters of sampling stations, 2009, 2010, 2012, and 2016. See Figures 2-7 for detail.

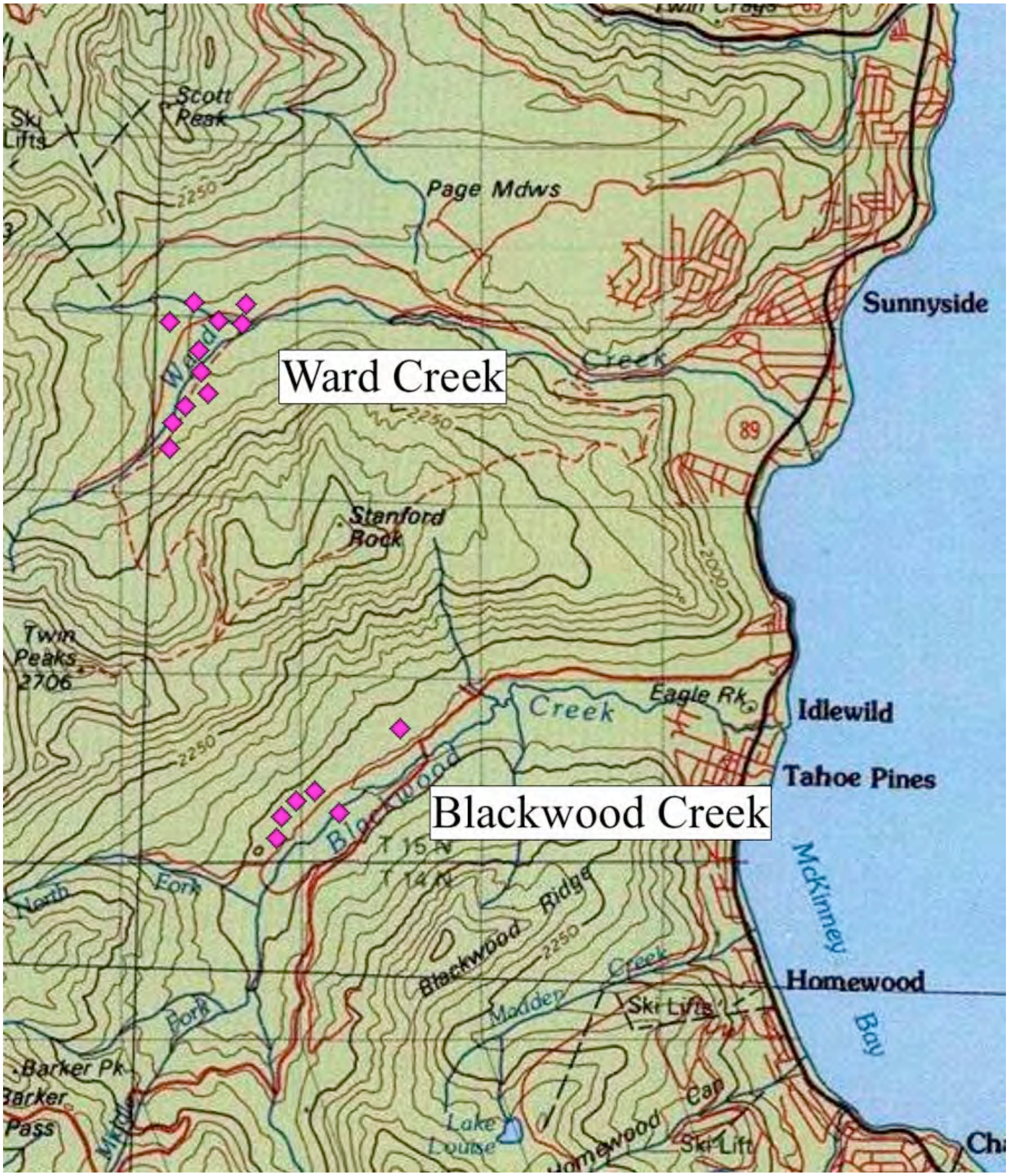


Figure 2. Detail of point count stations for Ward Creek and Blackwood Creek sampling clusters. Six of the Ward Creek stations were treated between the 2009 and 2010 sampling seasons, and one station was treated between the 2012 and 2016 seasons. The Blackwood Creek stations began receiving treatment after the 2010 sampling season. Ward and Blackwood stations were sampled in 2009, 2010, 2012, and 2016.

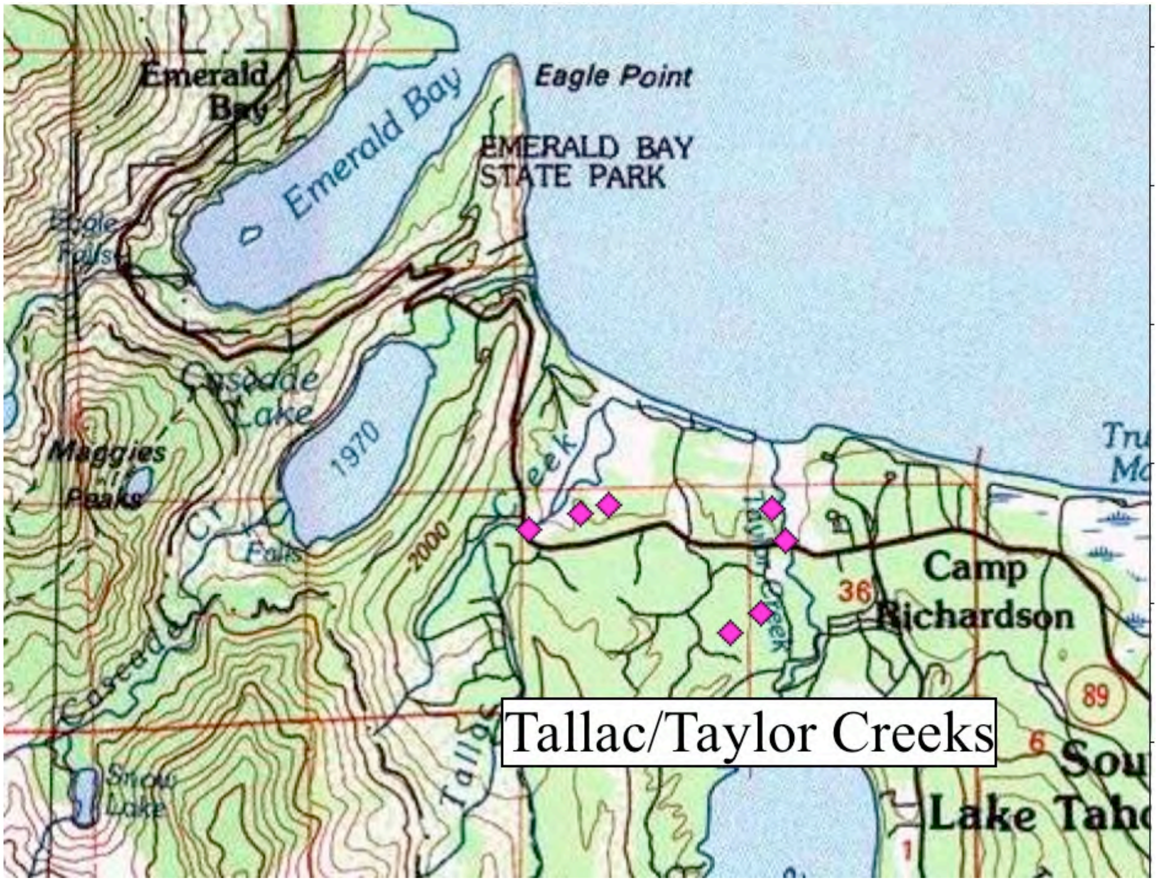


Figure 3. Detail of Tallac/Taylor Creek point count cluster. These sites began receiving treatment after the 2010 sampling period. These stations were sampled in 2009, 2010, 2012, and 2016.

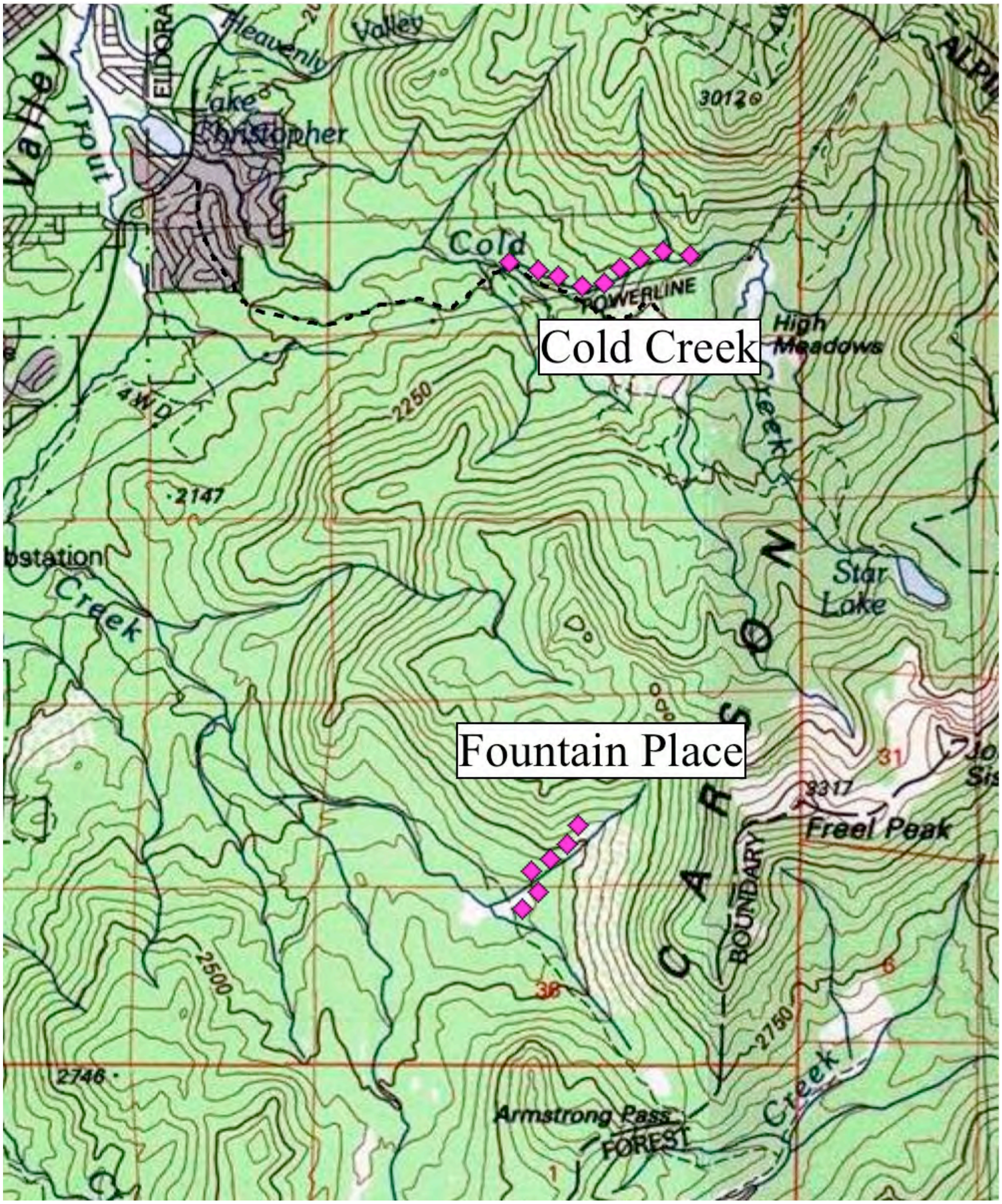


Figure 4. Detail of Cold Creek and Fountain Place point count clusters. Three of the Cold Creek stations were treated between 2009 and 2010 sampling seasons, and the rest may receive treatment at a later date. Fountain Place, originally slated for treatment, has remained a control. Cold Creek stations were sampled in 2009 only. Baseline data exist for Fountain Place from 2002-2004; these were resampled in 2016.

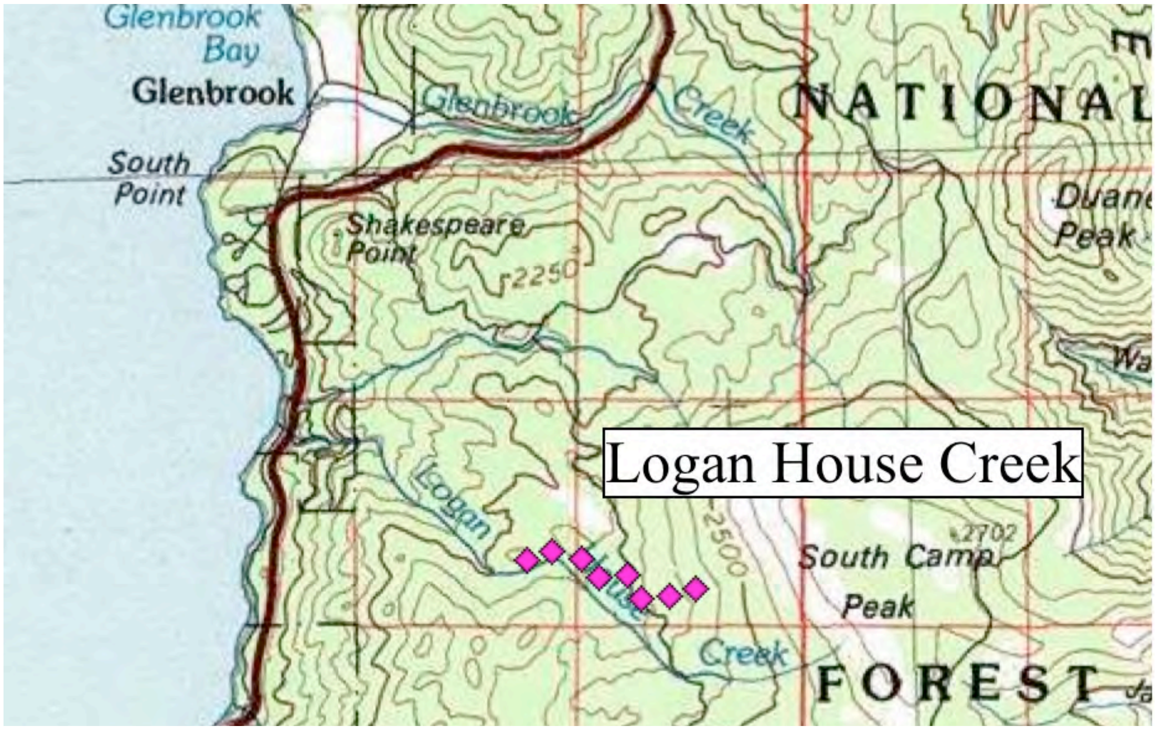


Figure 5. Detail of Logan House Creek sampling cluster. These point count stations are not slated for treatment and will serve as a control. This cluster was sampled in 2009 and 2016, and baseline data exist for 2002-2004.

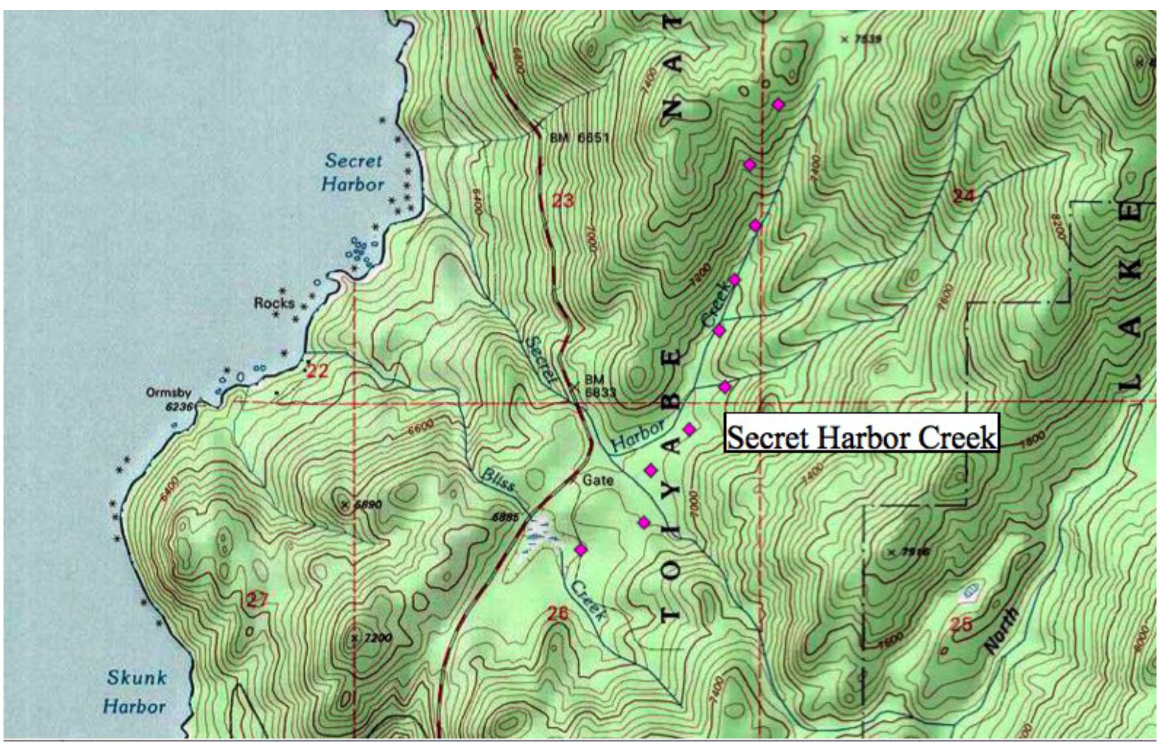


Figure 6. Detail of Secret Harbor Creek sampling cluster. Four of these stations were treated in late 2010. This cluster was sampled in 2012 and 2016, and baseline data exist for 2009.

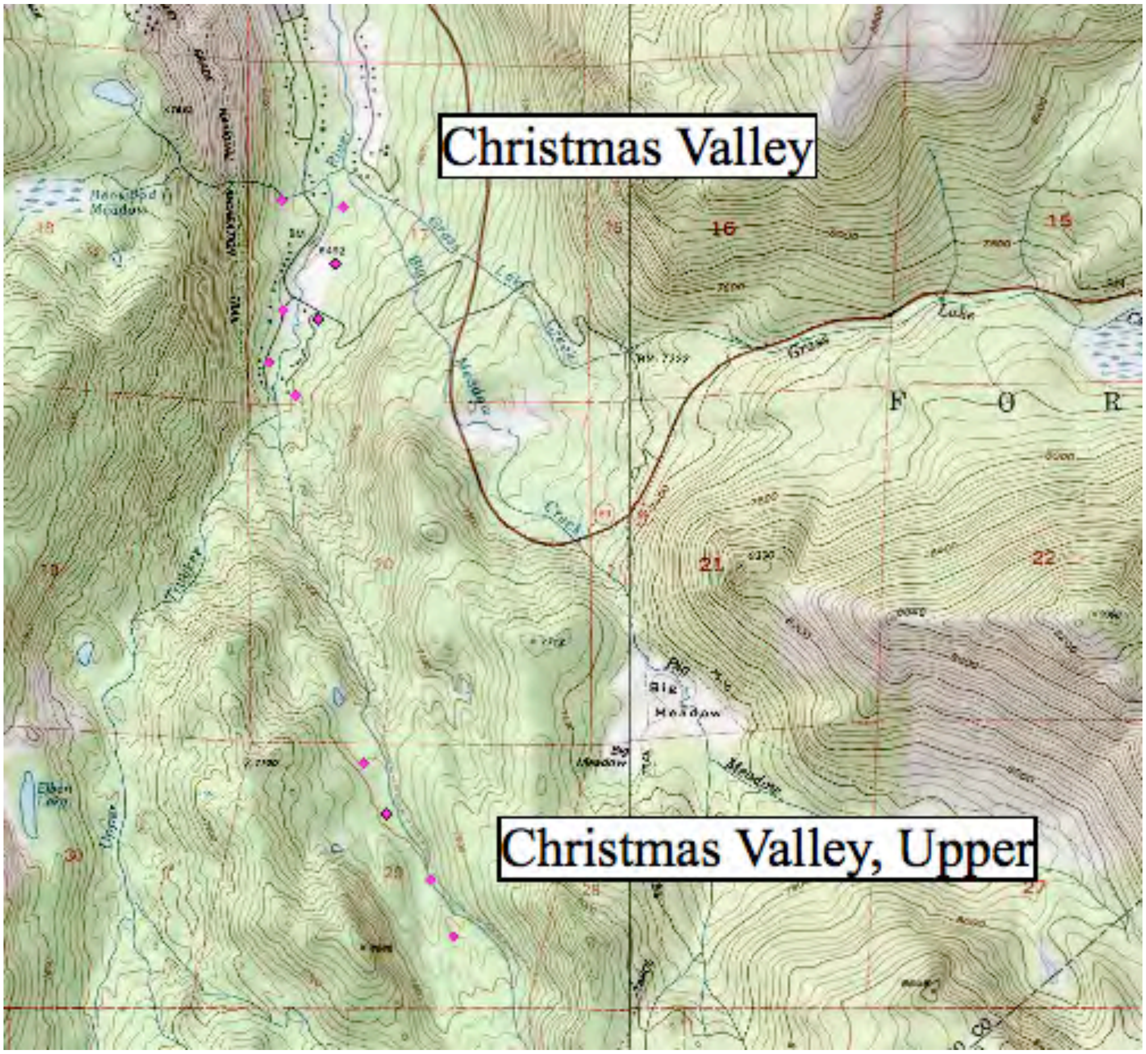


Figure 7. Detail of Christmas Valley sampling clusters. Christmas Valley stations were sampled in 2009 and 2010. The Christmas Valley, Upper stations were initiated in 2010 and resampled, after treatment, in 2012 and 2016.

Figure 8. Beaver (*Castor canadensis*) activity at one of the Taylor Creek sites altered the habitat considerably between 2012 and 2016, necessitating a reassessment of habitat variables.

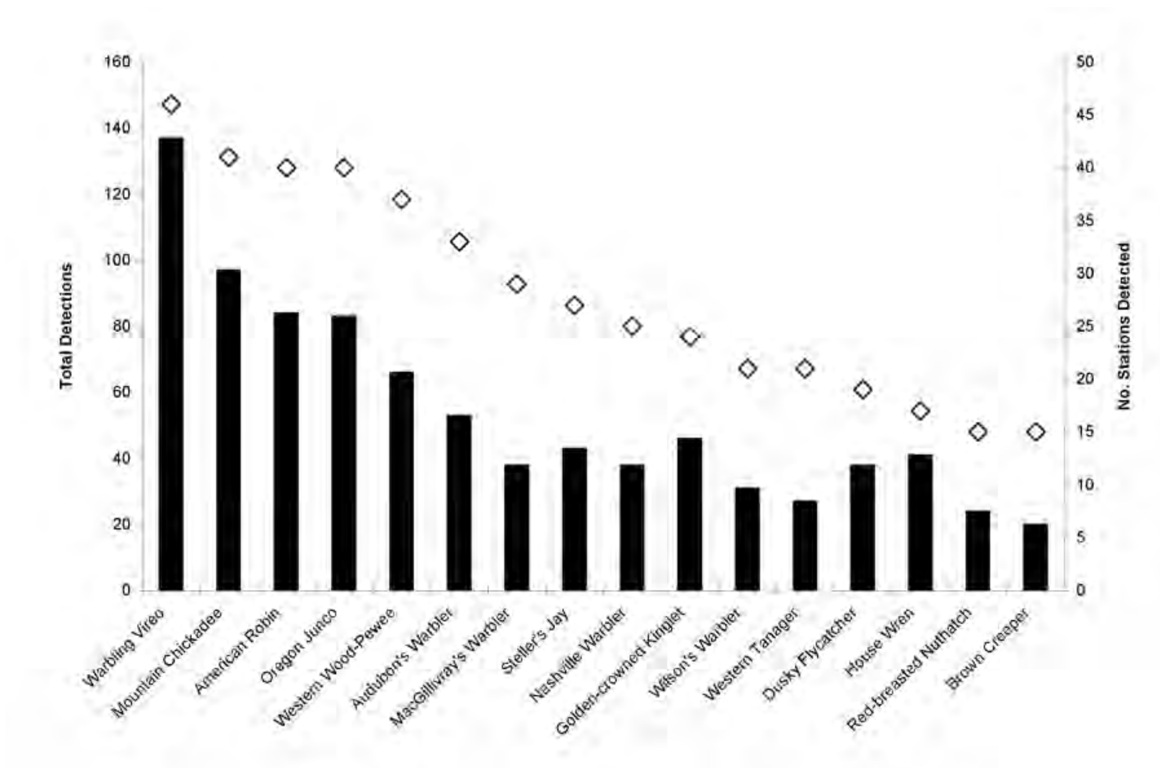


Figure 9. Total detections (bars) and number of stations detected (diamonds) for the 16 most commonly encountered and abundant species in 2009, for observations ≤ 50 m from point count center.

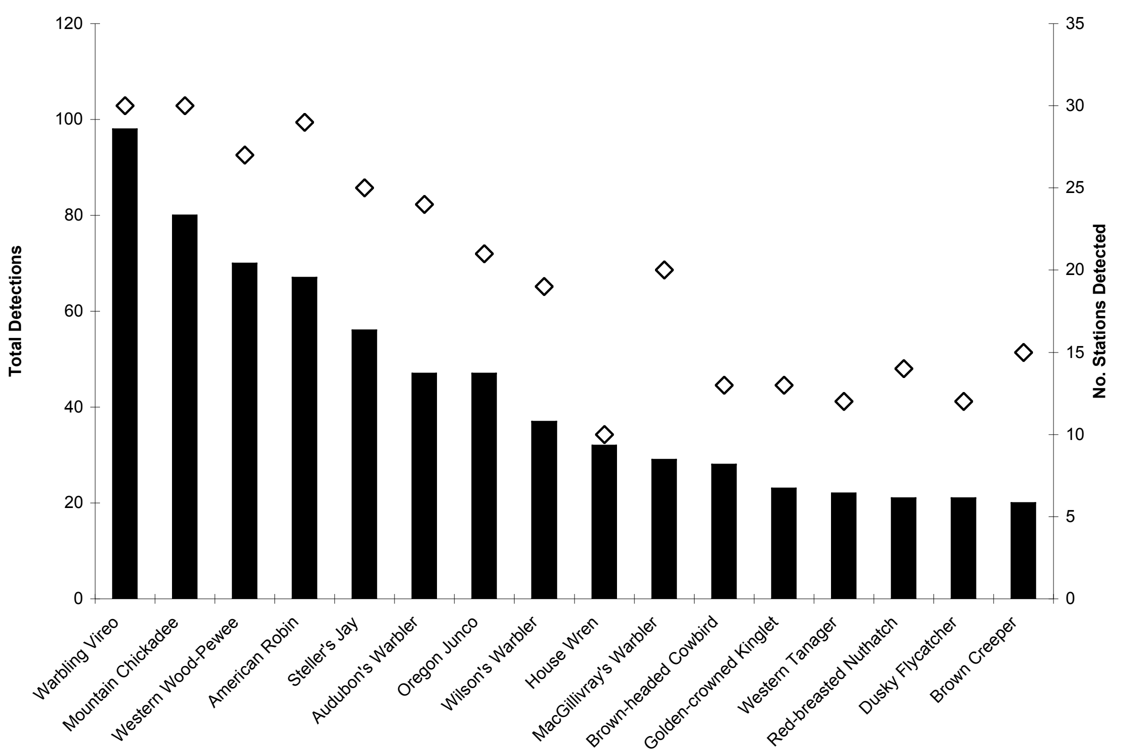


Figure 10. Total detections (bars) and number of stations detected (diamonds) for the 16 most commonly encountered and abundant species in 2010, for observations ≤ 50 m from point count center.

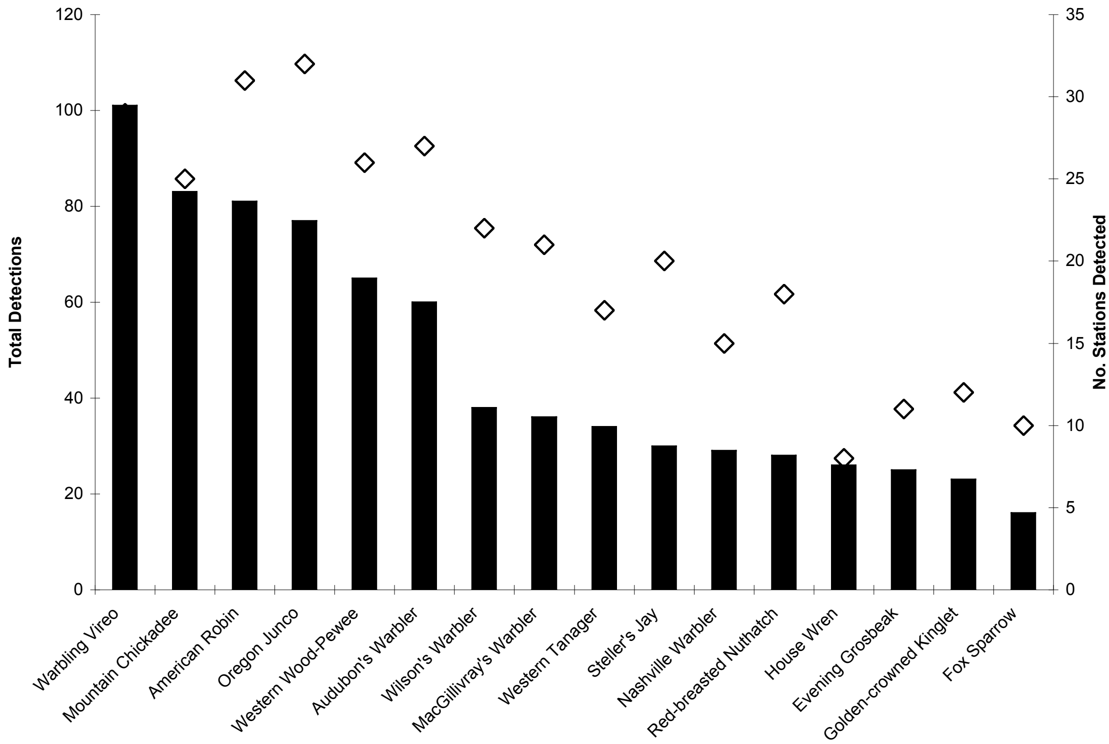


Figure 11. Total detections (bars) and number of stations detected (diamonds) for the 16 most commonly encountered and abundant species in 2012, for observations ≤ 50 m from point count center.

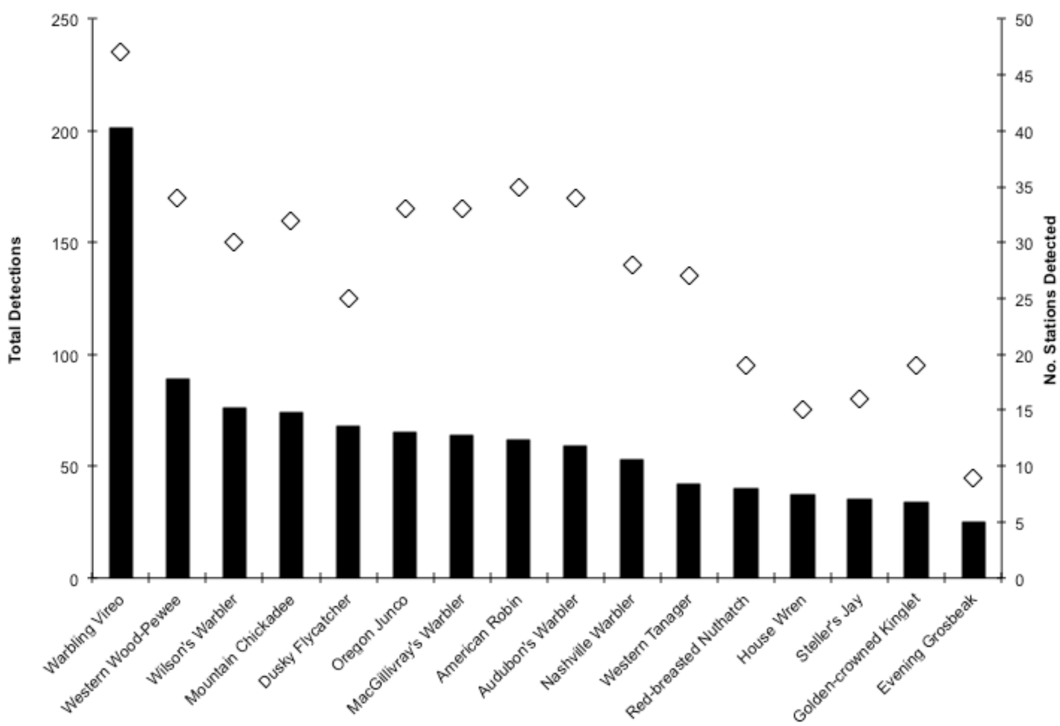


Figure 12. Total detections (bars) and number of stations detected (diamonds) for the 16 most commonly encountered and abundant species in 2016, for observations ≤ 50 m from point count center.

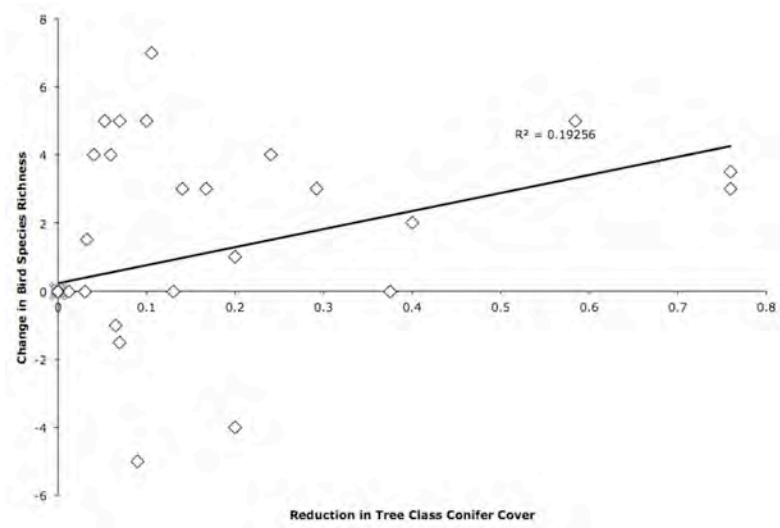
Figure 13. Root suckering and spontaneous crown regeneration in a decadent small diameter aspen two years after heavy mechanical conifer thinning in Blackwood Canyon. Photo taken 22 June 2012.

Figure 14. Heavy aspen root suckering and growth 6 years after mechanical conifer removal in Blackwood Canyon. Some of this new growth has experienced deer browse, though much less than seen in the Carson Range. Photo taken 26 June 2016.

a.

b.

Figure 15a. Aspen root suckering directly beneath an burn pile scar at Secret Harbor Creek, 21 June 2012. Typical of Carson Range regeneration, this sucker appears to have experienced considerable browse, presumably from deer. Once the herbacous understory fills in around them, such heavily browsed aspen suckers are favored by nesting MacGillivray's Warblers and Dusky Flycatchers.
Figure 15b. Multiple generations of root suckers establishing in Tallac Creek Meadow in the absence of cattle grazing, 4 July 2012.



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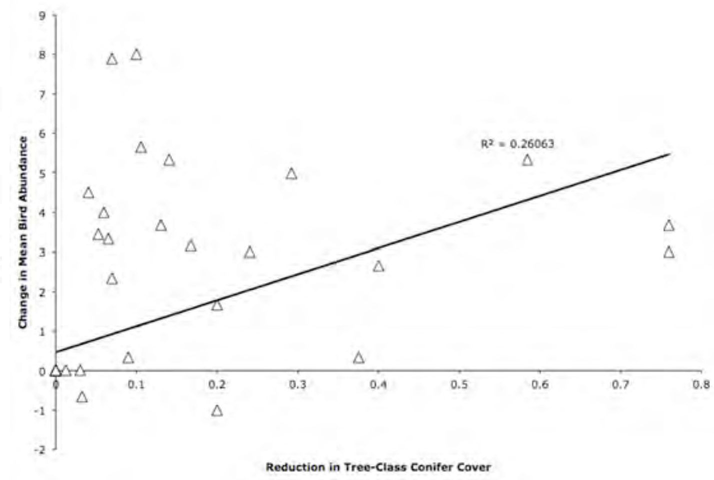
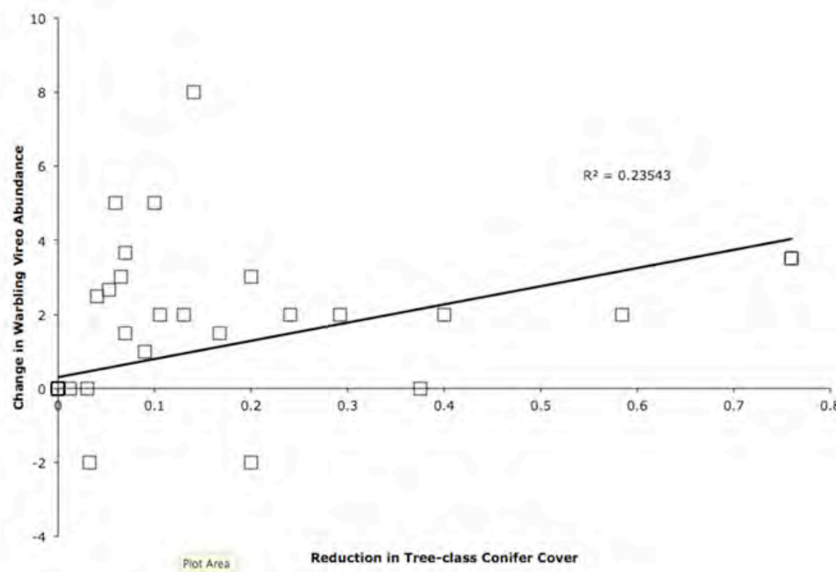


b.

Figure 16. Relationships between reduction in absolute tree-class conifer cover (%) and increase in primary bird indices. Figure 16a. Positive relationship with Bird Species Richness (R^2 =0.19256). Figure 16b. Positive relationship with Mean Bird Abundance (R^2 =0.26063).



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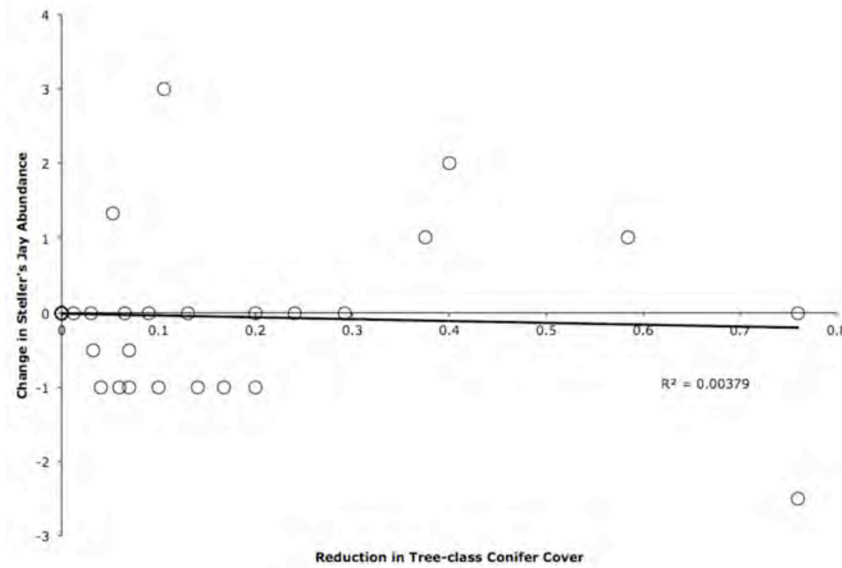

b.

Figure 17. Relationships between reduction in absolute tree-class conifer cover (%) and abundances of key bird species. Figure 17a. Slightly positive relationship with Warbling Vireo (R^2 =0.2543). Figure 17b. Slightly negative relationship with Steller's Jay (R^2 =0.00379).

Figure 18. Steller's Jay depredating a Warbling Vireo nest at a Tunnel Creek study site in July 2008 during fieldwork for Richardson (2010).

Table 1. Stations sampled and treatment status per treatment cluster per year (2002-2016). Pre-treatment data from 2002-2004 (inclusive) and 2008 were from previous research projects.

Years	2002-2004	2008 [b]	2009		2010		2012		2016	
Treatment Status	Pre-	Pre-	Pre-	Post-	Pre-	Post-	Pre-	Post-	Pre-	Post-
Cluster (*n*)										
Blackwood Creek (6)			6		6		2	4	0	6
Christmas Valley (7)			7		7					
Christmas Valley, Upper (4)					4			4		4
Cold Creek (9)			9							
Fountain Place (6)[c]	6		6						6	
Logan House Creek (8)[c]	8	8	8						8	
Secret Harbor Creek (10)		10					6	4	6	4
Tallac/Taylor Creeks (7)			5	2[d]	5	2	1	6	1	6
Ward Creek (11)			11		5	6	5	6	5	6
Total (annual total)	14	18	52	2 (54)	29	6 (35)	16	22 (38)	26	26 (52)

[a] Data from 2002-2004 were collected as part of a separate study (Richardson and Heath 2004).

[b] Data from 2008 were collected as part of a separate study (Richardson 2010).

[c] All or most of the stations in this cluster can serve as control to separate treatment and year effects, as no treatments are planned at these sites.

[d] Two stations were treated in 2004. No pre-treatment bird survey data exist, but we were able to incorporate Years Post Treatment as a variable into models examining treatment effects.

Table 2. Environmental and habitat variables used in model selection to predict bird species richness (BSR), mean bird abundance (MBA), and Warbling Vireo, Steller's Jay, and Douglas' Squirrel abundance from point count data in aspen stands, Lake Tahoe Basin, 2009-2016. Tree-class conifer cover, for example, represents an estimate of absolute cover, over the 50 m radius plot, of all coniferous species, above 5 m in height. Shrub-class aspen cover, on the other hand, represents an estimate of absolute cover, over the 50 m radius plot, of all aspen plants between 0.5 and 5 meters in height. Model abbreviations in parentheses.

Habitat Variable	Units	Description
Tree-class cover (Tree) [a]	%	Absolute cover of all tree species, above 5 m
Tree-class conifer cover (Conifer)	%	Abs. cover of all conifer trees, above 5 m
Tree-class aspen cover (Aspen)	%	Abs. cover of all aspen, above 5 m
Canopy cover (Canopy)	%	Spherical densiometer, mean, four readings
Shrub cover (Shrub)	%	Abs. cover of all woody veg., 0.5 -5 m
Shrub-class aspen cover (ShrAsp)	%	Abs. cover of all aspen, 0.5 –5 m
Shrub-class *Salix* cover (Willow)	%	Abs. cover of all willow, 0.5 –5 m
Herbaceous cover (Herb)	%	Abs. cover of herbaceous, below 0.5 m

[a] Tree-class cover was removed from all full models due to consistent, severe multicollinearity with tree-class conifer cover, tree-class aspen cover, or both.

Table 3. Bird species observed during 5-minute point counts at Lake Tahoe aspen habitat, 2009-2016. Species excluded from statistical analyses are marked with asterisk ((*) see METHODS: Data Analysis for details).

Common Name	*Scientific Name*
*Canada Goose	*Branta canadensis*
*Mallard	*Anas platyrhynchos*
*Common Merganser	*Mergus merganser*
*Mountain Quail	*Oreortyx pictus*
*Sooty Grouse	*Dendragapus fuliginosus*
*Sharp-shinned Hawk	*Accipiter striatus*
*Northern Goshawk	*A. gentilis*
*Bald Eagle	*Haliaeetus leucocephalus*
*Sora	*Poranza carolina*
*Spotted Sandpiper	*Actitis macularius*
*Wilson's Snipe	*Gallinago delicata*
Band-tailed Pigeon	*Columba fasciata*
*Great Horned Owl	*Bubo virginianus*
*Northern Pygmy-Owl	*Glaucidium gnoma*
*Northern Saw-whet Owl	*Aegolius acadicus*
Rufus Hummingbird	*Selasphorus rufus*
Calliope Hummingbird	*Stellula calliope*
Red-breasted Sapsucker	*Sphyrapicus ruber*
Williamson's Sapsucker	*S. thyroideus*
Downy Woodpecker	*Picoides pubescens*
Hairy Woodpecker	*P. villosus*
White-headed Woodpecker	*P. albolarvatus*
Black-backed Woodpecker	*P. arcticus*
Red-shafted Flicker	*Colaptes auratus collaris*
Pileated Woodpecker	*Dryocopus pileatus*
Olive-sided Fycatcher	*Contopus cooperi*
Western Wood-Pewee	*C. sordidulus*
Willow Flycatcher	*Empidonax trailli*
Dusky Flycatcher	*E. oberholseri*
Solitary Vireo	*Vireo plumbeus/cassinii* [a]
Warbling Vireo	*V. gilvus*
Steller's Jay	*Cyanocitta stelleri*
Clark's Nutcracker	*Nucifraga columbiana*
*Common Raven	Corvus corax
Tree Swallow	*Tachycineta bicolor*
Mountain Chickadee	*Poecile gambeli*
Red-breasted Nuthatch	*Sitta canadensis*
White-breasted Nuthatch	*S. carolinensis*
Pygmy Nuthatch	*S. pygmaea*
Brown Creeper	*Certhia americana*
Pacific Wren	*Troglodytes pacificus*

Table 3 (cont'd).

Common Name	*Scientific Name*
House Wren	*T. aedon*
Golden-crowned Kinglet	*Regulus satrapa*
Ruby-crowned Kinglet	*R. calendula*
Townsend's Solitaire	*Myadestes townsendi*
Swainson's Thrush	*Catharus ustulatus*
Hermit Thrush	*C. guttatus*
American Robin	*Turdus migratorius*
Orange-crowned Warbler	*Oreothlypis celata*
Nashville Warbler	*O. ruficapilla*
Yellow Warbler	*Dendroica petechia*
Audubon's Warbler	*D. coronata auduboni*
Hermit Warbler	*D. occidentalis*
MacGillivray's Warbler	*Oporornis tolmiei*
Wilson's Warbler	*Wilsonia pusilla*
Western Tanager	*Piranga ludoviciana*
Green-tailed Towhee	*Pipilo chlorurus*
Spotted Towhee	*P. maculatus*
Chipping Sparrow	*Spizella passerina*
Fox Sparrow	*Passerella iliaca*
Song Sparrow	*Melospiza melodia*
Lincoln's Sparrow	*M. lincolnii*
Mountain White-crowned Sparrow	*Zonotrichia leucophrys oriantha*
Oregon Junco	*Junco hyemalis thurberi*
Black-headed Grosbeak	*Pheucticus melanocephalus*
Lazuli Bunting	*Passerina amoena*
Red-winged Blackbird	*Agelaius phoeniceus*
Brewer's Blackbird	*Euphagus cyanocephalus*
Brown-headed Cowbird	*Molothrus ater*
Pine Grosbeak	*Pinicola enucleator*
Cassin's Finch	*Carpodacus cassinii*
Red Crossbill	*Loxia curvirostra*
Pine Siskin	*Spinus pinus*
Lesser Goldfinch	*S. psaltria*
Evening Grosbeak	*Coccothraustes vespertinus*

[a] Most individuals were positively identified to *V. cassinii*, but recent influxes of *V. plumbeus* into the Carson Range dictated a conservative approach, and assignment to the species-pair for purposes of analysis.

Table 4. Summary statistics of mean bird abundance (MBA) for each sampling cluster. See Figures 1-7 for location information. Note: each point count station is meant to be an independent sample; stations within a given cluster may be in separate stands or in different parts of the same stand, but subject to different levels of encroachment/treatment. Any interpretation of cluster-level statistics must bear that in mind.

	2002-2004 MBA	2009 MBA	2010 MBA
Cluster (*n*)	Mean ± SE (Range)	Mean ± SE (Range)	Mean ± SE (Range)
Blackwood Creek (6)	not sampled	6.33 ± 0.43 (5.00-8.00)	6.50 ± 0.36 (5.33-7.67)
Christmas Valley (7)	not sampled	6.57 ± 0.52 (4.33-8.33)	9.52 ± 0.96 (6.00-14.00)
Christmas Valley, Upper (4)	not sampled	not sampled	7.92 ± 1.24 (4.33-10.00)
Cold Creek (9)	not sampled	3.54 ± 0.30 (2.33-5.67)	not sampled
Fountain Place (6) [a]	9.35 ± 2.48 (3.00-21.33)	6.28 ± 1.42 (3.67-12.67)	not sampled
Logan House Creek (8)[a]	13.46 ± 1.51 (5.67-18.00)	9.08 ± 1.01 (6.33-15.33)	not sampled
Secret Harbor Creek (10) [b]	not sampled	not sampled	not sampled
Tallac/Talor Creeks (7)	not sampled	10.14 ± 0.60 (7.33-12.00)	8.43 ± 0.88 (5.33-11.00)
Ward Creek (11)	not sampled	6.58 ± 0.58 (4.00-9.33)	7.94 ± 0.72 (4.33-12.00)

[a] All stations in this cluster serve as control to separate treatment and year effects

[b] Stations also were sampled in 2008. MBA for was 9.50 ± 1.55 (2-20)

	2012 MBA	2016 MBA
Cluster (*n*)	Mean ± SE (Range)	Mean ± SE (Range)
Blackwood Creek (6)	8.94 ± 1.20 (5.00-13.00)	10.28 ± 0.88 (8.67-14.33)
Christmas Valley (7)	not sampled	not sampled
Christmas Valley, Upper (4)	7.83 ± 1.06 (5.67-10.67)	10.17 ± 2.68 (6.00-18.00)
Cold Creek (9)	not sampled	not sampled
Fountain Place (6) [a]	not sampled	6.06 ± 1.06 (3.00-10.00)
Logan House Creek (8)[a]	not sampled	11.17 ± 1.25 (6.00-16.00)
Secret Harbor Creek (10)	6.00 ± 1.15 (1.67-10.67)	4.43 ± 0.74 (1.00-9.33)
Tallac/Talor Creeks (7)	10.71 ± 0.92 (7.00-14.67)	9.90 ± 1.69 (4.00-17.33)
Ward Creek (11)	9.48 ± 0.73 (6.00 - 13.33)	9.02 ± 0.92 (5.00-13.33)

[a] All stations in this cluster serve as control to separate treatment and year effects

Table 5. Summary statistics of breeding species richness (BSR) for each sampling cluster. See Figures 1-7 for location information. Note: each point count station is meant to be an independent sample; stations within a given cluster may be in separate stands or in different parts of the same stand, but subject to different levels of encroachment/treatment. Any interpretation of cluster-level statistics must bear that in mind.

	2002-2004 BSR	2009 BSR	2010 BSR
Cluster (*n*)	Mean ± SE (Range)	Mean ± SE (Range)	Mean ± SE (Range)
Blackwood Creek (6)	not sampled	10.33 ± 0.76 (8-12)	11.17 ± 0.79 (8-13)
Christmas Valley (7)	not sampled	11.71 ± 0.92 (8-15)	13.71 ± 0.52 (12-16)
Christmas Valley, Upper (4)	not sampled	not sampled	13.25 ± 1.89 (8-16)
Cold Creek (9)	not sampled	6.89 ± 0.54 (5-10)	not sampled
Fountain Place (6) [a]	5.67 ± 1.09 (2-9.33)	10.83 ± 1.19 (7-14)	not sampled
Logan House Creek (8)[a]	8.08 ± 0.69 (4.67-10)	15.00 ± 1.20 (11-22)	not sampled
Secret Harbor Creek (10) [b]	not sampled	not sampled	not sampled
Tallac/Talor Creeks (7)	not sampled	14.14 ± 1.22 (9-19)	12.00 ± 0.93 (9-16)
Ward Creek (11)	not sampled	11.45 ± 0.85 (8-17)	11.18 ± 0.83 (7-15)

[a] All stations in this cluster serve as control to separate treatment and year effects

[b] Stations also were sampled in 2008. Mean BSR for 2008 was 7.00 ± 0.91 (1-10)

	2012 BSR	2016 BSR
Cluster (*n*)	Mean ± SE (Range)	Mean ± SE (Range)
Blackwood Creek (6)	12.50 ± 1.20 (8-16)	14.33 ± 0.71 (11.00-16.00)
Christmas Valley (7)	not sampled	not sampled
Christmas Valley, Upper (4)	9.50 ± 1.04 (7-12)	12.50 ± 2.96 (8.00-21.00)
Cold Creek (9)	not sampled	not sampled
Fountain Place (6) [a]	not sampled	9.83 ± 1.08 (6.00-13.00)
Logan House Creek (8)[a]	not sampled	15.75 ± 1.03 (11.00-20.00)
Secret Harbor Creek (10)	9.80 ± 1.71 (4-17)	7.70 ± 1.01 (3.00-14.00)
Tallac/Talor Creeks (7)	14.71 ± 0.87 (11-17)	13.14 ± 1.67 (8.00-18.00)
Ward Creek (11)	13.73 ± 1.11 (8 - 20)	12.82 ± 0.67 (10.00-17.00)

[a] All stations in this cluster serve as control to separate treatment and year effects

Table 6. Habitat parameters retained in optimal regression models predicting (a) MBA, (b) BSR, (c) Warbling Vireo abundance, (d) Steller's Jay abundance, and (e) Douglas' Squirrel abundance, in aspen habitats, Lake Tahoe Basin, 2002-2016. P-values are from test that parameter = 0.

Variable	Estimate	SE	t-value	P-value
(a) MBA	($F_{5,63}$ = 24.46, p <0.001)			
(intercept)	5.04	0.75	6.75	<0.001
Tree-class Aspen	2.24	1.34	1.67	0.097
Tree-class Conifers	- 3.48	1.36	2.56	0.011
Shrub	0.05	0.01	3.67	<0.001
Herb	0.06	0.01	6.15	<0.001
Shrub-class Aspen	-9.90	2.72	3.64	<0.001
(b) BSR	($F_{4,64}$ = 19.42, p <0.001)			
(intercept)	5.51	1.10	5.01	<0.001
Tree-class Conifers	- 2.15	1.44	1.50	0.136
Shrub	0.03	0.01	2.37	0.018
Herb	0.07	0.01	6.86	<0.001
Shrub-class Willow	-7.24	2.76	2.63	0.009
(c) Warbling Vireo	($F_{4,64}$ = 20.24, p<0.001)			
(intercept)	0.78	0.55	1.42	0.158
Tree-class Aspen	4.55	0.84	5.18	<0.001
Shrub	0.02	0.01	2.11	0.037
Herb	0.01	0.01	1.80	0.073
(d) Steller's Jay	($F_{4,64}$ = 3.49, p=0.017)			
(intercept)	0.31	0.25	1.24	0.218
Tree-class Aspen	- 1.40	0.51	2.75	0.006
Herb	0.01	<0.01	1.96	0.052
Total Canopy	0.01	<0.01	2.24	0.026
(e) Douglas' Squirrel	($F_{3,65}$ = 14.64, p<0.001)			
(intercept)	0.12	0.36	0.33	0.742
Tree-class Aspen	- 0.48	0.49	0.91	0.366
Tree-class Conifers	3.12	0.54	5.76	<0.001

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