Differences in avian community structure and biodiversity following a Sudden Aspen Decline in Southwest Colorado

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ABSTRACT

Aspen (*Populus tremuloides)* stands in southwestern Colorado have recently experienced sudden aspen decline (SAD), which is the rapid mortality of aspen forest on a landscape scale. Studies on bird populations indicate higher avian biodiversity associated with aspen habitat; yet, no research has been published on avian community changes associated with SAD. Therefore, from early June to early July 2009 and 2010, we conducted avian surveys and evaluated SAD intensity in aspen stands located in the Dolores Ranger District of the San Juan National Forest. We classified different SAD levels that included: 1) Low SAD (0-30%), 2) moderate SAD (30.1-70%), and 3) high SAD (70.1-100%). We evaluated avian species richness and diversity among different SAD levels, performed an indicator species analysis, and analyzed use of SAD habitat by foraging guilds. Avian species richness and diversity was significantly greater in stands with high SAD than in stands with low SAD. Similarly, the greatest number of indicator species, species that are particularly faithful to a SAD level, was associated with high SAD in 2009 and 2010. Also, obligate insectivores and species with diets composed of > 75% invertebrates were more abundant in high SAD than in low SAD. Our data suggests that the initial changes in avian community structure associated with SAD are distinct between low and high SAD stands, and that stands experiencing high SAD support greater avian biodiversity during the early stages of this disturbance due to forest structure changes in aspen overstory and potential new food sources.

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There is a growing body of evidence documenting an emerging trend of climate-mediated forest dieback in woodland and savanna ecosystems worldwide (Allen et al. 2010). This large-scale decline in global forest cover is thought to result from higher global temperatures and altered regional precipitation patterns (Allen et al. 2010). Such wholesale changes in forest structure are likely to have profound implications for terrestrial wildlife communities.

In the intermountain west of North America, forest dieback from Sudden Aspen Decline (SAD) is of particular concern. SAD is defined as a synchronous pattern of rapid aspen (*Populus tremuloides*) branch dieback and crown thinning associated with landscape-scale tree mortality, which is not caused by primary pathogens and insects (Worrall et al. 2008, Worrall et al. 2010). This climate-mediated disturbance results from a combined degradation of aspen from heat stress and from various biotic agents that are not typically associated with aspen mortality (Worrall et al. 2008). Heat stress from recent drought conditions (2000-2005) destabilized aspen stands, leaving them susceptible to secondary biotic agents that include aspen bark beetles (*Trypophloeus populi* and *Procryphalus mucronatus*), poplar borer beetles (*Saperda calcarata*), bronze poplar borer beetles (*Agrilus liragus*), and cytospora canker (*Valsa sordida*) (Worrall et al. 2008, Worrall et al. 2010). Evidence for the climate-related association lies in the fact that SAD-related aspen mortality was found to be greater at lower elevations, on southern to western aspects, and in mature stands with lower densities, where existing heat levels are comparatively higher (Worrall et al. 2008, Worrall et al. 2010). SAD loss is exacerbated by an associated lack of suckering beneath failing stands. Aspen regeneration typically occurs vegetatively after a disturbance, via a large interconnected root system that sends up root suckers (Schier et al. 1985). However, sucker densities in SAD-impacted stands have been found to be lower than in unaffected aspen stands (Worrall et al. 2008, Worrall et al. 2010). With a lack of suckering from healthy root systems to regenerate stands, forest cover will likely convert to conifer-dominated vegetation types in areas where aspen stands have been eliminated by SAD (Shepperd et al. 2001).

Aspen has the widest distribution of any native tree in North America (Jones 1985). Within Colorado, there are more than one million acres of aspen forest (Jones 1985). Approximately 17% of forest cover in Colorado has been impacted by SAD, and aspen stands in southwestern Colorado have experienced the greatest occurrence of SAD in the state (Worrall et al. 2010).

Aspen is a keystone species in the Intermountain West, and aspen habitat is considered to be exceptionally diverse, providing high-quality habitat to a variety of plants and animals (Debyle 1985, Mueggler 1985). In fact, research has shown significant biodiversity loss associated with conversion from aspen to other forest cover (Bartos and Campbell 1998a, b). In particular, studies on bird populations indicate greater species richness and abundance associated with aspen forests compared with most other North American montane habitats (Salt 1957, Flack 1976, Winternitz 1980, Debyle 1985, Griffis-Kyle and Beier 2003). Also, research has demonstrated that these biodiversity values are significantly higher in aspen than in neighboring conifer stands (Turchi et al. 1995, Richardson and Heath 2004). Specific benefits that aspen habitat confers to avian communities include herbaceous layers that provide food and shelter opportunities, increased insect production, thermal cover, moisture retention, and favorable

nesting sites for cavity-nesting avian species (Verner 1988). Thus, aspen is a unique and necessary component of conifer-dominated montane ecosystems in the West because it provides a haven of avian diversity that is disproportionate to surrounding vegetation types.

The primary objective of our study was to evaluate differences in avian species composition and diversity across a SAD gradient following a SAD disturbance in southwestern Colorado. To accomplish this objective, our research had two main goals: 1) to quantify SAD-related changes in forest structure, and 2) to collect avian survey data to determine initial avian community changes associated with SAD over a two-year period within the region. We hypothesized that there would be a decrease in avian biodiversity as SAD level increased, given the affinity of many avian species for aspen habitat. Previous literature regarding SAD has focused on the causes and distributions of the disturbance; yet, evaluations of community-level responses to SAD have not currently been published.

METHOD

Study sites and selection criteria

We conducted our study within the Dolores Ranger District of the San Juan National Forest (SJNF), given that a larger percentage of aspen cover has been lost here due to SAD (~10%) than in any other location in Colorado (Worrall et al. 2008). This portion of the SJNF is located in the southwestern-most extent of the San Juan mountain range of southwest Colorado (Fig. 1). We employed a stratified random sampling design by selecting stands composed of >95% aspen overstory to maintain homogeneity among stands. We also controlled for slope, aspect, and elevation (2600 m to 3000 m range) during stand selection. Stands were defined as any area of contiguous aspen forest with relative similarities in tree species composition and height. Sixty sample points were randomly located within these stands to establish a plot center for both the avian and the vegetation circle plots. Randomization of plot centers was achieved using ArcGIS software (ArcGIS: Release 9.3. Redlands, California: Environmental Systems Research Institute, 1999-2009) and Hawth's Analysis Tools (Beyer 2004) to randomly locate an initial plot within each stand from which a transect was paced out and plot centers were located every 200 m along the transect. Transects were terminated at distances ≥ 50 m from stand perimeters. The sample point locations were classified based on the percentage of SAD in each plot (stems with SAD agent detected/total stems in plot) into one of 3 levels: 1) Low SAD (0-30%), 2) moderate SAD (30.1-70%), and 3) high SAD (70.1-100%). There were 20 sample points for each level.

Vegetation survey protocol

At the center of each sample point, a 16 m diameter circular plot was established to collect overstory data on all stems ≥ breast height (1.37 m) and with a diameter at breast height (dbh) ≥ 5cm, including: 1) species, 2) tree condition (evaluated based on the US Forest Service tree status scale {1 = live, 2 = declining, 3 = recent snag, 4 = loose bark snag, 5 = clean snag, 6 = broken above breast height, 7 = broken below breast height}), 3) dbh (cm, measured for all tree species present, plots >99% aspen cover), 4) tree canopy height (m) (measured with a hypsometer), 5) SAD agent presence (0 = not present, 999= present, codes used by USFS for SAD monitoring), and 6) type of SAD agent when present (agents recorded: aspen bark beetles, poplar borer beetles, bronze poplar borer beetles and Cytospora canker). We used a 50-m transect intersecting the circle plot centers (transects placed parallel to the environmental gradient, with 0-m at the top of the slope, 25-m at plot center, and 50-m at the slope base) to

record canopy cover (0 = no canopy, 1= canopy) with a mirror densitometer at 16 points every 3 meters along the transect. We used overstory data to calculate SAD percentage (stems with SAD agent detected/total stems in plot), stand density (total stems/ha), and stand basal area (based on dbh) for each plot. Additionally, at the center point of each circular plot we recorded aspect, slope (measured with a hypsometer), and elevation (measured with a Garmin 360 SCX GPS unit, Garmin International, Inc., Olathe, KS, USA) and used the GPS unit to ascertain plot center coordinates for future monitoring. We monumented plot centers for re-measurement with rebar.

Avian survey protocol

We conducted avian censuses during the breeding season from 05 June to 09 July, 2009, and from 01 June to 10 July, 2010. Surveys were conducted from sunrise until ~ 11:00 a.m. Two avian surveys were completed per year for each sample point location, including the initial surveys beginning in early June of each year, and a second set of surveys beginning two weeks later. This spacing ensured that we captured early season and late season breeders. Data from these separate counts were then averaged for individual analyses of the 2009 and 2010 surveys. To prevent biases that could occur due to time-of-day bird activity levels, locations that were initially surveyed in the early half of the morning (sunrise to ~ 8:30 a.m.) were randomly chosen to be surveyed the second time during the latter half of the morning (8:30 to ~ 11:00 a.m.) and vice versa. Surveys were conducted at each of the 60 sample point locations using a modified version of the standard point count method (Ralph et al. 1993). From a fixed center position, five minute interval counts were used to record all species detected visually or aurally, except when it was evident that an individual was using the habitat for hunting only (e.g. flyovers). Only unique individual detections were recorded, and detection distance was also estimated and plotted on data maps for each observation to aid in awareness of previous detections. Point counts were initiated immediately upon arrival, and any species that flushed upon approach were included in the point count data if their location of first detection fell within the plot boundary. Observations were all made by the same observer (SPB) in 100 m fixed-radius plots. Given the patchy distribution of aspen forest habitat here, we were not able to maintain the recommended minimum distance in wooded areas of 250 m (Ralph, et al. 1993) between sample points for every survey. However, a 200 m minimum distance should be sufficient, given that 98 percent of our detections occurred at distances $\leq$ 75m, and 92 percent occurred at distances $\leq$ 50 m. Also, due to the discontinuous aspen forest habitat, we were limited to a 50 m minimum distance to stand edges in some plots. To control for species using external habitat, detections that were known to originate outside stand perimeters were omitted in the cases when our 100 m radius plot extended beyond stand edges. During periods of rain, fog, or high winds (> 13 km/hr), surveys were not conducted. However, cloud cover and temperature were not considered as survey restrictions, given that temperatures during our study were relatively consistent and that cloud cover conditions were continually variable in this mountainous terrain.

Point counts are the most efficient and favorable method for forest avian surveys, yet they can misrepresent quiet, loud, nocturnal, or flocking species (Ralph, et al. 1993). However, we assumed equal detection of these species for the following reasons: 1) flocking species were not detected during any of our surveys, 2) ninety-two percent of detections occurred at distances $\leq$ 50 m, which would increase detectability of quiet species and allow for better discrimination of louder species, and 3) we did not include nocturnal species.

Statistical Analysis

Vegetation data from individual plots were averaged for analysis among the three SAD levels (n = 20). Mean vegetative structure differences among the different SAD levels were

analyzed using multiple Kruskal-Wallis one-way analysis of variance (ANOVA) tests. A Bonferroni post-hoc pairwise comparison of the different SAD levels was also used to assess whether vegetation variables were significantly different across all SAD levels.

To evaluate different biodiversity measures across SAD levels, we calculated two diversity indices, the Shannon-Weaver Diversity Index (calculated as e^H) and the Simpson's Index of Diversity, and determined species richness values for each plot. These values were averaged amongst the three SAD levels for analysis (n = 20). To analyze mean differences in species richness and the two diversity indices among the different SAD levels, we used multiple Kruskal-Wallis one-way ANOVA tests, followed by Bonferroni post-hoc comparison tests. We also organized species into guilds based on foraging strategies and used multiple Kruskal-Wallis tests and Bonferroni comparisons to analyze differences in mean abundance among SAD levels by species using different foraging strategies.

To examine species-specific changes associated with SAD, we performed a MONTE CARLO test of significance of observed maximum indicator values for each species detected (McCune and Grace 2002), which uses indicator values based on bird abundance and frequency to identify species that are particularly consistent indicators for different SAD levels. Indicator values were compared to random trials (1000 Monte Carlo randomizations) to determine *P*-values for each species (McCune and Grace 2002). Indicator species were defined as species where $P \leq 0.05$ and indicator value > 25 (INDVAL = relative abundance x relative frequency, INDVAL range = 0 to 100) (Dufrene and Legendre 1997).

RESULTS

Vegetation

Differences were detected in aspen forest structure across the SAD gradient during the vegetation surveys conducted in 2009 (Table 1). Canopy cover and tree status were significantly different among all SAD levels and had similar *P*-values (Table 1), suggesting autocorrelation between these variables. Canopy cover decreased as SAD level increased, and tree status (more advanced snag condition) increased with SAD level increases. Stand density and basal area were lower in areas of high SAD and significantly different between low to moderate SAD and low to high SAD levels (Table 1). DBH differed significantly between low and high SAD levels and was greater in high SAD stands (Table 1). Slope differed significantly between moderate and high SAD levels (Table 1). This was an expected outcome because one plot in the moderate SAD level had a relatively high gradient (21%), which may have skewed the results for slope. However, all other slopes had a grade $\leq$ 10 percent, which should have minimal impacts on avian distributions. Tree height and aspect were not significantly different among SAD levels (Table 1).

Avifauna

We detected a total of 26 species in all SAD stands (n = 60) for 2009 and 2010 combined (Table 2, Appendix 1). Only two species in 2009 and four species in 2010 had < 5% observations and, therefore, were not included in indicator species analysis. These species had low detection rates over the course of the study. Five species abundances' differed significantly across the SAD gradient and were determined to be indicator species for a particular SAD level. There was one indicator for low SAD (2009) and four indicators for high SAD (2009 and 2010) (Table 2).

Species richness differed significantly among SAD levels for both years (2009: $n = 20$, H = 12.127, $P = 0.002$; 2010: $n = 20$, H = 8.640, $P = 0.013$), with significantly greater species richness occurring in high SAD stands than in low SAD stands ($P_{2009} = 0.001$, $P_{2010} = 0.007$, Fig.2A). The two diversity indices (Shannon-Weaver Diversity Index {e^H} and Simpson's Index of Diversity {D}) were also significantly different among SAD levels for both years (e^H_{2009}: $n = 20$, H = 11.2130, $P = 0.004$, e^H_{2010}: $n = 20$, H = 10.930, $P = 0.004$, D_{2009}: $n = 20$, H = 9.210, $P = 0.010$, D_{2010}: $n = 20$, H = 13.045, $P = 0.001$), with high SAD stands having larger diversity values than other SAD levels (Figs. 2B, 2C). Significant differences for these indices were detected between low and high SAD (e^H: $P = 0.0020$, *D:* $P = 0.0060$) and low and moderate SAD levels (e^H: $P = 0.0190$, *D:* $P = 0.0050$) in 2009 (Figs. 2B, 2C). However, significant differences for these indices were detected between low and high SAD levels (e^H: $P = 0.001$, *D:* $P = 0.003$) in 2010 (Figs. 2B, 2C). There was some temporal variation within the species richness and diversity index values between 2009 and 2010; however, this difference was not significant ($P_{richness} = 0.679$, $P_{eH} = 0.247$, $P_D = 0.184$).

We found significant differences of avian responses to SAD when species were organized into foraging strategy guilds. We found that obligate insectivorous species, and species whose diet is largely dependent upon insects (> 75%), had significant differences in abundances among SAD levels in 2009 and 2010 ($2009_{obligate}$ $n = 20$, H = 15.017, $P = 0.001$; $2010_{obligate}$ $n = 20$, H = 10.327, $P = 0.006$; $2009_{>75}$ $n = 20$, H = 19.810, $P < 0.000$; $2010_{>75}$ $n = 20$, H = 10.852, $P = 0.004$; Figs. 3A, 3B). These differences were significant between low and high SAD for both years ($P_{2009obligate} < 0.000$, $P_{2010obligate} = 0.020$, $P_{2009>75} < 0.000$, $P\ P_{2010>75} < 0.002$), and avian abundance was greater in high SAD. Additionally, in 2009, species with diets primarily of invertebrates were significantly more abundant in moderate SAD stands than in low SAD stands ($P = 0.023$). Yet, in the 2010 analysis, obligate insectivorous species were significantly more abundant in moderate SAD stands than in low SAD stands ($P = 0.030$). Species with diets that are less dependent upon insects (< 75% of diet) did not demonstrate significant differences in abundance among SAD levels in 2009 or 2010 (2009: $n = 20$, H = 3.780, $P = 0.151$; 2010: $n = 20$, H = 3.624, $P = 0.163$; Figs. 3A, 3B).

DISCUSSION

Differences were detected in forest vegetation structure among low, moderate and high SAD stands. These differences can profoundly influence avian community distributions in SAD-affected aspen forests of southwest Colorado because SAD-related changes can alter snag abundance, canopy cover, understory vegetation, and other avian habitat factors. Many of the unique characteristics of high SAD stands were predictable responses to an increase in aspen mortality. For example, increased tree status (snag level) and decreased percent canopy cover are intuitive because these characteristics correspond with an increase in aspen mortality. Also, the greater average DBH values and the observed lower stand density and basal area in high SAD stands are consistent with results presented by Worrall et al. (2008). Their results indicated that larger trees were more prone to SAD events perhaps due to decreased stress tolerance associated with maturity. Worrall and others (2008) also found that stands with lower densities were more susceptible to SAD occurrences due to the increased propensity for heat to infiltrate more open stand structures.

Contrary to our hypothesis, avian biodiversity was greater in areas that have experienced high SAD, as indicated by associated higher mean species richness and diversity values, as well as the greater abundance of indicator species in high SAD. The significantly greater biodiversity

values found in high SAD stands suggests that certain avian species are responding to the newly-available niches provided by changes associated with SAD.

One characteristic of high SAD stands that may be exerting a strong influence on avian distributions, especially on cavity nesting species, is the increased magnitude of snags. Cavity nesters typically utilize snags for nest sites, and studies have indicated a strong association between cavity nesters and snags (Scott 1979, Raphael and White 1984, Zarnowitz and Manuwal 1985, Dobkin et al. 1995, Martin et al. 2004, Hollenbeck and Ripple 2006). Similar to our results, Zarnowitz and Manuwal (1985) found that species richness, density, and diversity values for cavity nesting birds were greater in areas with higher concentrations of snags. Given the affinity of cavity nesting birds for snags, cavity nester population responses strongly influenced the species richness and diversity measures in our results. Indeed, three of the four species identified as indicator species for high SAD levels were primary or secondary cavity nesters—the northern flicker, the violet-green swallow, and the house wren. Since indicator analyses are based on abundance and frequency data for a particular species, our results suggest that these species' responses to snags may be playing a critical role in the observed differences in biodiversity between low and high SAD stands. However, for some cavity-nesting species, the number of available snags is not the only important characteristic to consider. The size of the snag may also play a critical role for woodpeckers according to Flack (1976), who found that woodpeckers primarily utilize snags with a DBH > 15cm. Since the mean DBH in our stands for the low, moderate, and high SAD levels was > 15 cm, the snags identified in our study are likely to be suitable for woodpeckers. Future studies should evaluate nest hole frequency among the different SAD levels to confirm that the snags identified in our study are being utilized by cavity-nesting birds. Snags may also be valuable to aerial insectivores within SAD stands such as western wood peewees (*Contopus sordidulus*) and swallows (F. Hirundinidae), since these species utilize snags for perch sites from which they hunt their prey (Hutto 1995).

Another important vegetative characteristic identified in high SAD stands that may be attracting aerial insectivores was low stand density and basal area, implying a more open forest structure than low and moderate stands. Western wood-peewees prefer open forests and woodlands, and previous studies on burn treatments and timber harvests indicate an increase in their abundance associated with these types of disturbances (Garrison et al. 2005, Kirkpatrick et al. 2006). Additionally, previous work by Rendell and Robertson (1989) indicates that swallows frequently choose cavity nest sites in snags that are in open stands. SAD may be a new type of disturbance that is generating a niche of open forests in the region that these species are currently exploiting.

Changing forest structure associated with SAD disturbances may result in decreased abundance of canopy-nesting species, such as warbling vireos (*Vireo gilvus*). Warbling vireos commonly favor nest sites with canopy cover, which is believed to provide thermoregulation and protection from heat stress (Walsberg 1981). The warbling vireo was the only species that responded with a significant decrease in abundance as SAD increased in 2009, which may relate to decreased canopy cover. However, this pattern was not detected in the 2010 analysis. These differences in warbling vireo response to SAD may be related to a pattern of habitat use that has not been detected during the limited period of this study; thus, long-term demographic data is needed.

Increased avian biodiversity in high SAD stands may relate to greater forage availability from higher insect productivity associated with SAD disturbances. Since borer and bark beetle infestations are one of the conditions associated with SAD (Worrall et al. 2008), an increase in

these wood-boring arthropod populations can be assumed. Thus, insectivorous avian species, especially woodpeckers, may be responding to SAD-meditated increases in prey abundance. It has been well-documented that many woodpeckers are attracted to recently-burned areas because of several factors that include an associated increase in wood-boring beetle abundances (Amman & Ryan 1991, Hutto 1995, Murphy and Lehnhausen). It may be the case that woodpeckers and other insectivorous species are attracted to SAD due to similar associated increases in prey abundance. Our guild analysis seems to support this hypothesis since there were higher abundances of insectivorous species in high SAD habitat than in low SAD habitat; however, species that supplemented their diet with other food sources (e.g. fruit, sap, seeds) did not seem to discriminate among varying SAD levels. Therefore, future work is needed to evaluate invertebrate abundance in different SAD levels, to determine if there is higher invertebrate abundance in high SAD, and of what species of invertebrates, to help determine what food sources are available and which avian species will benefit.

There was some temporal variation in avian species' abundances within different SAD level habitat in the SJNF between 2009 and 2010 (Table 2, Appendix 1). Therefore, surveys for each year were not collated for analysis. This variation is expected, given the transient nature of succession associated with aspen forest disturbances, in which aspen cover removed by a disturbance can regenerate quickly, or can be replaced by conifer saplings in fairly short timeframes. However, there were strong similarities of overall patterns in species richness and diversity, as well as comparative stability of indicator species abundances, indicating general response patterns of avian species to different SAD levels.

Several avian species identified in this study did not appear to respond to SAD (Appendix 1). These species may not have been greatly affected by the changes associated with the occurrence of SAD. More importantly, we had comparatively smaller sample sizes for some of these species which resulted in a relatively low statistical power to detect significant differences in species abundance among the different levels of SAD. This may particularly be the case for other cavity-nesting species identified in the study that did not demonstrate significant differences in abundance.

Management Implications

Our results suggest that habitat conditions associated with SAD disturbances may be important response drivers for certain avian species using aspen habitat in the SJNF, and may ultimately influence avian community distributions in the region if SAD continues to afflict healthy aspen. Our results also imply that certain avian species may be selecting SAD habitat based on food availability and vegetation structure, which can lead to greater avian diversity in SAD-affected areas. Since this increased diversity can be related to changes associated with SAD, it is important for forest managers to maintain some of this transitional forest habitat until stands progress to early seral stages and natural reforestation occurs. However, some partially SAD-afflicted stands are currently being harvested immediately to promote regeneration of aspen clones, in an effort to preserve aspen at a landscape scale. Therefore, we recommend a multi-faceted approach to managing aspen stands afflicted by SAD. For example, sections of SAD-affected forest could be left un-harvested to maintain a vegetation patch mosaic at a landscape scale. Alternatively, progressive timber harvest treatments can be used to restore aspen regeneration while leaving some standing snags on site for use by cavity nesting species. For example, shelterwood cutting may be a useful method for regenerating aspen stands while promoting both vegetative and avian diversity (King and DeGraaf 2000, Goodale et al. 2009). Northern flickers have been found to utilize regenerating aspen habitat that had lingering

standing snags (Kirk et al. 1996), and this pattern may be reflected by other cavity nesting species. Other researchers have recognized the value of retaining snags as sources of habitat in the landscape and have made similar management suggestions to leave snags un-harvested after fire disturbances, and to re-evaluate the clear-cutting of forests after disturbances (Hutto 1995).

Continued monitoring of indicator species for different SAD levels is recommended, especially warbling vireo populations, since this species seems potentially sensitive to increases in SAD. Caution should be used when generalizing our results, especially to a landscape scale. Since all data were generated and analyzed at a site scale, landscape level changes are not well addressed. Also, our results cannot be applied to regional nocturnal avian species, since night surveys were not conducted. In addition, it is important to note that the list of indicator species identified in this study may not be an exhaustive list of species associated with changes in SAD. There is reason to believe that additional indicator species may be identified if higher abundances of all species were detected to provide greater statistical power for these species. This is probably especially true for cavity nesting species that were detected in our study, but had low statistical power due to minimal detections. Also, species abundance patterns may not always reflect habitat quality; therefore, future work should evaluate impacts of SAD on both reproductive success and predator-prey dynamics, to determine the overall consequences of SAD to avian fitness and habitat.

CONCLUSION

Our study determined differences in avian species composition, abundance and biodiversity associated with sudden aspen decline (SAD) in southwest Colorado. Our research provides insight on avian community responses to future SAD disturbances. Climate models anticipate higher temperatures and increasing aridity in western North America; thus, it is predicted that drought-induced aspen forest mortality will occur more frequently under future climate change scenarios (Hogg and Bernier 2005). Specifically, models by Worrall and others (2010) predict a recurrence of SAD under warmer and more arid growing seasons. Therefore, our study can help wildlife managers anticipate future changes in avian community distribution patterns associated with SAD. However, it is important to consider that this is an initial measure of avian changes associated with this ephemeral event. The vegetative conditions that contributed to increased avian diversity in the high SAD stands in our study will not remain in stasis. These stands will likely convert to conifer-dominated forests through natural successional processes, given a lack of aspen regeneration (Crawford et al. 1998, Rogers 2002, Worrall et al. 2010). These conifer-dominant forests will favor different avian communities. Therefore, this research should be extended into nearby warm-dry mixed conifer stands to forecast avian community composition patterns, given the wholesale loss of aspen at lower elevation sites. Also, long-term monitoring would help predict how forest birds might respond to the holistic changes that will likely occur as stands progress to early seral stages, adding long-term value to this initial measure of avian changes associated with SAD.

Acknowledgements

Funding for this project was provided by a Natural and Behavioral Sciences Grant, Fort Lewis College. We thank Joseph Ortega and Erin Lehmer for their contributions of time and knowledge to this project. We also thank the San Juan National Forest, Dolores Public Lands Office for providing maps, data, and background information on the San Juan National Forest.

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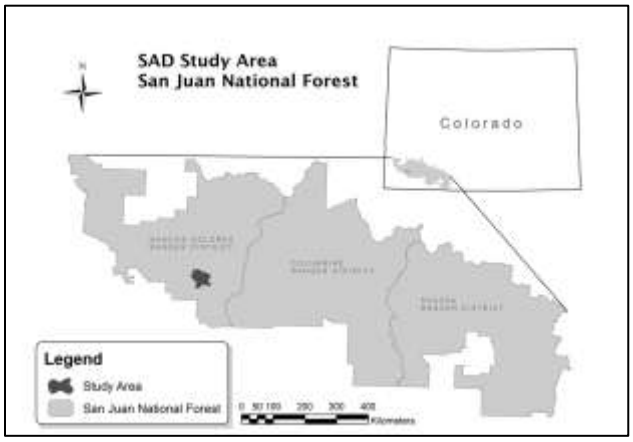

Fig. 1. Study location within the Mancos-Dolores Ranger District of the San Juan National Forest, Montezuma County, Colorado.

Table 1. Mean (± SE) differences in vegetation variables among low, moderate, and high SAD levels in 2009. Categories with the same letters are not significantly different at $p \leq 0.05$ by Bonferroni pairwise comparison tests. *P*-values determined using a non-parametric Kruskal Wallis test, *n* =20. Tree status evaluated based on the US Forest Service tree status scale (1 = live, 2 = declining, 3 = recent snag, 4 = loose bark snag, 5 = clean snag, 6 = broken above breast height, 7 = broken below breast height).

Vegetation variable	Low SAD	Moderate SAD	High SAD	H	*P*
% Canopy cover	81.54±2.00[a]	59.54±5.00[b]	33.10±4.00[c]	35.34	<0.000
Tree status	1.46±0.05[a]	2.43±0.08[b]	3.51±0.08[c]	50.95	<0.000
Basal area (m^2/ha)	54.01±5.05[a]	39.35±2.32[b]	41.32±3.15[b]	5.84	0.0520
Stand density (stems/ha)	1887.26±136.69[a]	1248.27±130.59[b]	1069.94±84.91[b]	18.85	<0.000
Tree height (meters)	11.96±0.52[a]	11.78±0.50[a]	13.45±0.80[a]	5.14	0.0770
DBH (centimeters)	17.19±0.97[a]	18.55±0.93[ab]	21.74±0.97[b]	10.17	0.0060
Aspect	258.60±8.98[a]	207.25±19.52[a]	225.00±19.79[a]	1.90	0.3880
Slope	4.95±0.61[ab]	5.62±0.89[a]	3.02±0.37[b]	10.50	0.0050

Table 2. Indicator species associated with different levels of SAD in the San Juan National Forest in 2009 and 2010. Indicator species analyzed with a Monte Carlo test of significance of observed indicator values, which identifies species that are consistent indicators for different SAD levels (Indicator value = species abundance x species frequency).

SAD Level	**Species**	**Common Name**	**Indicator Value (±1SD) (2009, 2010)**	***P* (2009, 2010)**
Low[a]	*Vireo gilvus*	Warbling Vireo	41.90±1.64, 38.3± 2.19	0.0004, 0.1072
High[a, b]	*Troglodytes aedon*	House Wren	42.60±2.99, 44.7±2.44	0.0190, 0.0016
High[a, b]	*Tachycineta thalassina*	Violet-green swallow	49.30±4.89, 29.5± 5.25	0.0004, 0.0501
High[a]	*Contopus sordidulus*	Western wood peewee	40.20±4.94, 33.7±4.62	0.0090, 0.0744
High[a, b]	*Colaptes auratus*	Northern Flicker	45.60±4.97, 63.3±4.80	0.0012, 0.0002

[a] indicates significant indicator species in 2009

[b] indicates significant indicator species in 2010

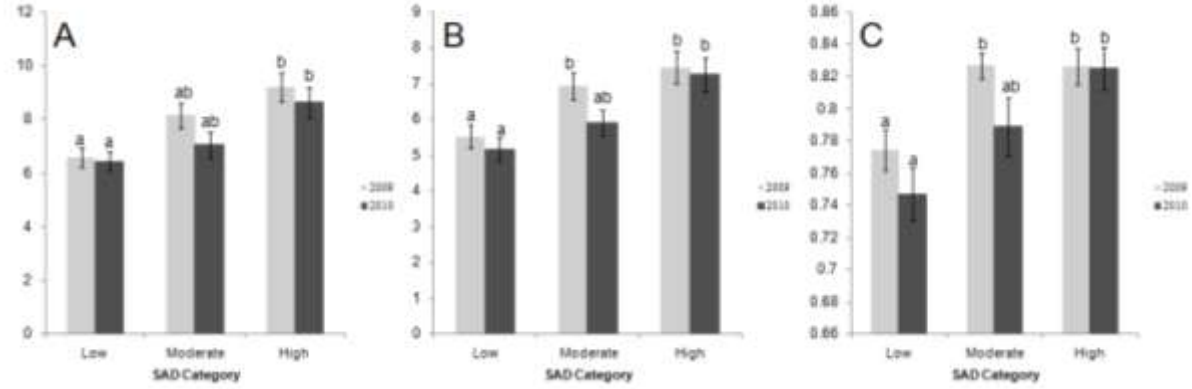

Fig. 2. Mean species richness (A), mean Shannon-Weaver Diversity Index (e^H) (B), and mean Simpson's Index of Diversity (C) at different SAD levels, determined from five minute point counts conducted in 2009 and 2010 on the San Juan National Forest in southwest Colorado. Error is presented as ± SE. Bars with the same letters are not significantly different among SAD levels within each year at $P \leq 0.05$ by Bonferroni pairwise comparison tests. *P*-values determined using a non-parametric Kruskal Wallis test, $n = 20$.

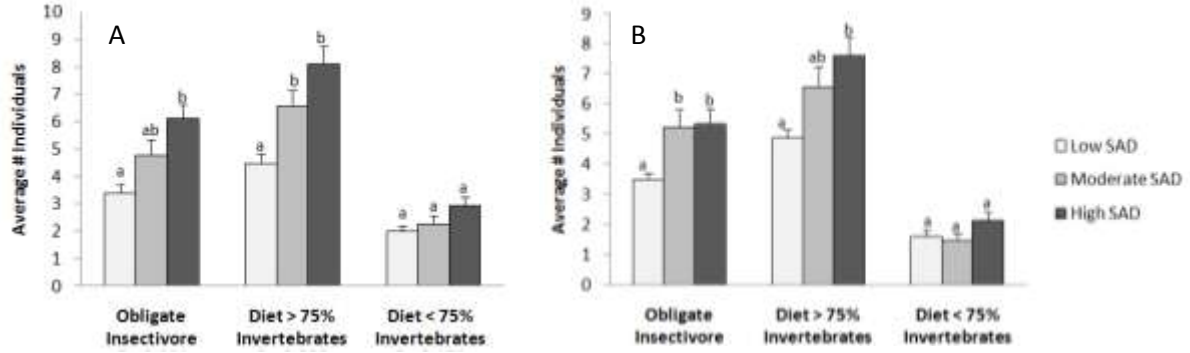

Fig. 3. Average number of individuals detected from three different feeding guilds at different SAD levels, determined from five minute point counts conducted in the San Juan National Forest during 2009 (A) and 2010 (B). Error is presented as ± SE. Bars with the same letters are not significantly different within a feeding guild among different SAD levels at $P \leq 0.05$ by Bonferroni pairwise comparison tests. *P*-values determined using a non-parametric Kruskal Wallis test, $n_{Obligate} = 5$, $n_{>75\%} = 12$, $n_{<75\%} = 9$.

Appendix 1
Species detected during point counts in the San Juan National Forest that were not identified as indicator species using a MONTE CARLO test of significance of observed indicator values (Indicator value = avian abundance x avian frequency).

Species	Common Name	Indicator Value (2009,2010)	*P* (2009, 2010)
Selasphorus platycercus	Broad-tailed hummingbird	12.6,19.8	0.5529, 0.4281
Sphyrapicus nuchalis	Red-naped sapsucker	13.9,10.0	0.3185, 0.6433
Picoides pubescens	Downy woodpecker	14.7,5.6	0.3675, 0.8702
Picoides villosus	Hairy woodpecker	13.3,11.2	0.3045, 0.3273
Corvus brachyrhynchos	American crow	10.3,5.0	0.4777, 1.0000
Progne subis	Purple martin	16.1,15.0	0.0816, 0.1096
Poecile gambeli	Mountain chickadee	9.1,6.4	0.7786, 0.8630
Sialia mexicana	Western bluebird	5.1	0.7614[a]
Sialia currucoides	Mountain bluebird	5.8	0.3243[a]
Turdus migratorius	American robin	27.3,26.2	0.3697, 0.6079
Catharus guttatus	Hermit thrush	31.1,13.9	0.2893, 0.8356
Vermivora celata	Orange-crowned warbler	21.1,19.0	0.2621, 0.5837
Dendroica coronata	Yellow-rumped warbler	21.8,37.2	0.4147, 0.1184
Dendroica petechia	Yellow warbler	22.1,7.5	0.1696, 0.8632
Wilsonia pusilla	Wilson's warbler	7.4	0.3237[a]
Piranga ludoviciana	Western tanager	2.6	1.0000[a]
Pipilo chlorurus	Green-tailed towhee	21.4	0.0338[b]
Melospiza lincolnii	Lincon's sparrow	9.8,7.3	0.3821, 0.7800
Junco hyemalis	Dark-eyed junco	27.6,17.3	0.8764, 0.5275
Molothrus ater	Brown-headed cowbird	10.0	0.4859[b]
Carduelis pinus	Pine siskin	14.9,25.0	0.3561, 0.0972

[a]Species had < five percent detections during 2010
[b]Species had < five percent detections during 2009