The conservation value of woody debris for cavity-nesting bees on

Boulder County Open Space

Final Report

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Abstract

Woody debris creates habitat for a number of animals including many of Boulder County's native pollinators. Cavity-nesting bees use holes created by other insects in trees and logs to nest in and provision pollen for their offspring; however little is known about the value of woody debris as habitat for bees on Boulder County Open Spaces, much less, if woody debris management practices are impacting the bee community. The goal of this study was to evaluate the conservation value of woody debris on 12 different Boulder County Parks and Open Space (BCPOS) riparian properties along the St. Vrain River. To do so, we estimated the quantity and quality of woody debris as bee nesting habitat at 23 sites, sampled the abundance and diversity of bees in each site, and investigated the relationships between woody debris and bee community dynamics using linear mixed modeling. Between May and September 2016, we sampled each site 6 times, using hand-netting to collect wild foraging bees and monitored two trap nests specifically for cavity-nesting bees. In total, we collected 3,662 bee specimens from netting, representing 33 bee genera and ~96 different species/morphospecies and recorded 664 individual bee nests within trap nests. Wood measurements suggested that areas where Open Space reported removing wood resulted in a 50% reduction in woody debris compared to unmanaged sites. Moreover, wood removal reduced overall bee abundance by 40%, though the pattern was driven mostly by a 41% reduction in non-cavity nesting bees compared to a 37% reduction in cavity nesting bees. Wood removal had no impact on netted genus richness, regardless of nesting preference. However, we did find a positive relationship between woody habitat availability and both total bee abundance and non-cavity-nesting bee abundance. Interestingly, wood removal increased colonization of bee blocks by some 16% compared to unmanaged sites, though we did not find a significant difference between managed and reduced sites. There was also a significant inverse relationship between bee nest abundance and woody debris. We interpret these results as suggesting that wood nesting bees are likely limited by suitable woody nesting habitat, and in areas where it is available prefer it over artificial nests. Conversely, where wood is lacking or must be removed, many cavity-nesting bees will readily nest in artificial substrates. Together, we feel our data strongly suggest that woody debris has both direct and indirect benefits for bee communities, and its management should be considered wherever pollinator conservation is a primary management goal. We also offer recommendations for BCPOS on the value of woody debris for native pollinator conservation, and means to preserve or enhance this habitat in the future.

Introduction

Riparian habitats are extremely important for many native pollinators, and in addition to floral resources also provide nesting habitat, such as vertical banks, open sandbars, and importantly, woody debris. Woody debris plays a number of roles in both terrestrial and aquatic ecosystems, including as reservoirs for carbon, as the nutritional basis for a variety of fungi, plants, and animals, and as habitat for many animals (Harmon et al. 2004), including many native bees. Colorado has an extremely diverse bee fauna with some 946 documented species, fifth in the U.S. for statewide diversity (Scott et al. 2011). Boulder County in particular has been studied for over 100 years, having been summarized in the early 1900's (Cockerell 1907), recently reviewed by Goldstein and Scott (Goldstein and Scott 2015), and highlighted for its potential to track long-term trends in bee diversity and community dynamics (National Research Council 2007). Moreover, nearly 30% of Boulder County's 562 reported bee species reproduce in wood, mostly in cavities made by other insects (Scott et al. 2011). These solitary bees build their nests in pre-existing cavities and provision pollen for their offspring inside. In time, as woody debris decays, it becomes available to other bee species that are capable of excavating cavities in softer wood (Figure S1). Cavity-nesting bees have even been suggested as bioindicators for tracking ecological change and habitat quality (Tscharntke et al. 1998), given their complex ecology and likely dependence on several aspects of ecosystem processes. Thus, woody debris likely contributes directly to the cavity-nesting bee species through providing nest habitat, but could additionally benefit all bees indirectly through other ecosystem functions, such as nutrient cycling, water retention, or through creating habitat heterogeneity.

Given the potential importance of woody debris for pollinators, surprisingly little is known about how it relates to bee communities. In general, studies have found that bee communities are often driven by the availability of nesting substrates (Potts et al. 2005, Murray et al. 2012). However, the value of woody debris for pollinator conservation is often overlooked by land managers, and the consequences of woody debris management are only just beginning to be explored. For instance, extraction of woody debris from an arid forest in Argentina tended to decrease the abundance of pollinators at flowers, although the effects of its removal declined with time (Vazquez et al. 2011). From studies in Europe, cavity-nesting bee and wasp communities do appear dependent on wood nesting substrates and other insects that bore into wood (Tscharntke et al. 1998, Westerfelt et al. 2015, Sydenham et al. 2016). However, little is known about the relationship between wood-nesting resources and bee communities here in the Front Range. Given the potential conservation value of woody debris as nesting sites, more studies are needed to determine the impacts of woody debris management on native pollinators.

This project aimed to determine the conservation value of woody debris on BCPOS riparian areas. To do so we used a combination of surveying techniques to 1) estimate the relative abundance and diversity of both cavity-nesting and other bees on open spaces along the St. Vrain Creek, 2) assess the quantity and quality of woody debris available as bee habitat as each site, and 3) explore the relationships between woody debris, its management, and pollinator abundance and diversity. The St. Vrain suffered catastrophic flooding in 2013, leaving some areas heavily littered with woody debris. Three years post-flooding, this woody debris could represent a boon in habitat for cavity-nesting bees, or a reduction of habitat where its removal was required. We hypothesized that riparian areas on BCPOS with more woody debris would support a greater abundance and diversity of cavity-nesting bees than areas where woody debris is scarce or has been removed.

Methods

Study Area

      The St. Vrain River was heavily impacted by the 2013 flood, which deposited high quantities of coarse woody debris (CWD) in riparian habitats adjacent to the river. We sampled 12 BCPOS-owned properties from the opening of the St. Vrain Canyon west of Lyons, eastward across the floodplain to the town of Longmont, CO (Table 1). To maximize sampling effort along riparian habitats we set up sampling points approximately every 500m along the creek (Figure 1). This design meant different numbers of sampling points at each property depending on size. Variations in the size and layout of each of the 12 properties required 4 sites at Hall Ranch, 3 sites at each of Hall Ranch 2, Pella Crossing, and Western Mobile, 2 sites at each of Gage, Golden-Fredstrom, and Keyes, and one site at Bullock, Wallace, Montgomery, Braly, and Ramey. These study sites had undergone various management practices regarding flood-deposited CWD, ranging from no management to complete wood removal. At each site within properties, we characterized wood management following notes from BCPOS personnel on wood management activities and from observations in the field (Table 1). Given the highly variable nature of woody debris management and our limited control over activities, we conservatively assigned sites as either "unmanaged", where there was no observed or reported wood removal, or "reduced", where woody debris was either removed through some portion of the area, piled together (therefore making some of it inaccessible), or otherwise reduced through management activities. After categorizing wood management, we ended up with 10 unmanaged sites and 15 reduced sites.

Woody Debris Sampling

      To estimate wood nesting resources, we established three 24m line-intercept transects at each site. We used bee blocks (see below) as a starting point for the three transects which were oriented at 20°, 150°, and 270°, respectively (Figure 2). Along each transect we recorded the location, length, and species of all woody debris ≥ 7.5 cm in diameter that intersected it. For each piece we measured the beginning and ending diameter of the debris and estimated the total volume of the debris using the following formula, where DS denotes the diameter of the small end, DL the diameter of the large end, and l the length of the piece of wood (modified from Woodall and Monleon 2008):

$$\frac{\left(\frac{\pi}{8}\right)(DS^2 + DL^2)l}{144}$$

      In addition, we identified the species of wood where possible, and categorized debris based on the stage of decay, ranked from 1 to 5 with 1 being sound and 5 being soft and powdery. We also inspected woody debris for signs of insect activity, recording existing cavities, their respective diameters, associated insects, etc. We made note of standing dead trees, large debris piles, and any other notable wood elements within the immediate vicinity. These detailed notes could be used to estimate the quality of woody debris types as habitat for native bees. Given that both nesting and floral resources are important in structuring pollinator communities,

we had originally planned to also record plant species richness along each transect, and estimate relative abundance of insect-pollinated plant species. However, due to logistical constraints, a lack of sufficient floral expertise, and the great deal of time devoted to wood and bee surveys, we decided to focus on the latter in hopes of better addressing our research goals within our timeframe and logistical means.

Pollinator Surveys

In total we installed 50 bee monitoring nests blocks across the 12 different properties (Table S1). We surveyed cavity-nesting bee communities with a combination of wooden nest blocks and bamboo nest bundles. Native bee nest blocks are an important monitoring and conservation tool (MacIvor and Packer 2015) and have been used to monitor bee community dynamics across space and time, and to explore the impacts of environmental change due to human activities (Gardner and Spivak 2014, Pereira-Peixoto et al. 2014). In addition, cavity-nesting species can often be determined by how they construct and seal off nests allowing us to use nest plug type as an index of cavity-nesting bee diversity (Rose et al. 2015). We constructed wooden blocks and bamboo bundles in early spring of 2016. Wooden blocks were constructed of 4"x6" untreated Douglas Fir. In each block we drilled 40 holes: 5 each of 8 different sizes ranging from 1/16" to 1/2" about 5" deep. Bamboo bundles were made of 40 bamboo pieces, about 5-6" in length, with the same number of diameters ranging from 1/16" to 1/2" held together in a wooden frame (Figure S2). The placement of each monitoring block was determined based on microhabitat availability within each site. A. Carper and V. Scott installed blocks between the 2nd and 4th of April 2016. At each of the 25 locations, we placed a pair of nest blocks (one wood and one bamboo) ~1 m off the ground, in full sun, and facing south to maximize visibility by bees and thus colonization (based on previous data).

We conducted a preliminary block check for early season bees on May 5th and 6th, followed by 5 additional rounds of block checks over 32 days of field work between 2nd June and 1st of Sept (hereafter "round"). During each round, we observed both types of trap nests and recorded data on each plug including its stage in construction, material of construction, depth, and signs of parasitism or emergence, and made note of any observed bee activity around the nests. Blocks were left in the field over fall and into winter to allow sufficient chilling for overwintering larvae and pupae, before being collected in January of 2017 and stored in Longmont, CO to avoid disturbance. Blocks were brought inside the lab in February and slowly warmed to instigate emergence. Every cavity in wooden blocks had a vial glued over them to capture emerging insects, while bamboo were placed in Ziploc bags. All were monitored daily throughout the summer and any newly emerged insects collected and labeled (including the type of block, site from which it was collected, and the diameter of the cavity in which it nested). All collected insects were then frozen and are currently being pinned, labeled, barcoded, and identified.

Given that cavity-nesting bee species are often not targeted in pollinator community surveys, in order to compare entire bee communities across sites we also hand-netted bees for 1 person-hour per round at each site. Combining these methods allowed us to assess the diversity of cavity-nesting species and also determine how much of the entire bee community they represent. During each round a team of observers walked haphazardly within 250m of each sampling location netting any bees that were seen visiting flowers or otherwise visible within the sampling area (excluding bees at trap nests). We netted for one hour per site, dividing the

sampling time by the number of observers (typically 2-3). Netting was conducted during days of fair weather (>23°C, mostly sunny, and light winds), between 9:00 and 16:00, times of peak bee activity. Netted bees were euthanized with ethyl acetate collecting jars and frozen before processing. All specimens were pinned, labeled, and uniquely barcoded. We identified netted specimens to the lowest taxonomic level possible. While species and morphospecies were possible for some genera, we conducted all analyses on genera level richness to avoid biasing results. We assigned genera as 'cavity-nester' or 'other' based on reported nesting habits for determined species we collected. While some genera, such as *Megachile*, can have both cavity- and ground-nesting species in addition to some species that nest in both substrates, the vast majority captured (>95%) were of cavity-nesting species. Therefore, we assigned the entire genus as cavity-nesters. For nest blocks, since processing is ongoing, we used nest plug material as an index for genus level determination, and ran our analyses on nest plug richness. All specimens are being identified and curated within the Entomology Section at the University of Colorado Museum of Natural History (CUMNH).

We supported our recorded observations with photographs of each block at each visit, and also photos of any interesting bee activity. Photos were taken with a Canon D70 digital SLR camera, fitted with a 50-270mm macro lens and ring flash. These photographs are being organized and catalogued at the Entomology Section and will aid in the analysis of nest plug composition and species determinations, as well as characterizing the surrounding habitat. We have collectively taken over 1,700 photographs with high resolution digital macrophotography, a number of videos of native bee cavity-nesting activity, and have many more cell phone photographs and videos. These media are of both scientific and conservation interest, given that they may capture new and interesting ecological interactions (e.g., Figure S3). A. Carper has set up a temporary Google Drive folder to share photos with BCPOS, pending the development of an online photo sharing server to be set up through the museum: (https://drive.google.com/open?id=0B9YTr_yuHmWGeGNaNmdCeFo2dnc) . We anticipate assigning media the same copyright as other media produced by the museum, a Creative Commons Attribution-NonCommercial license (CC BY-NC). This license allows the use of any media for non-commercial purposes as long as the images are attributed to the CUMNH.

Statistical Analyses

We conducted statistical analyses on sites from all but one property, Keyes, which had one unmanaged and one managed site but was so far removed from the others sites that ecologically it was very different and could skew results (*see* Figure 1). In addition, we excluded one other site at Western Mobile, site 26, given that we captured less than 50 specimens overall (an extreme outlier), and that both trap nests were torn down on several occasions, presumable by raccoons, limiting access by bees. We conducted all analyses in JMP Pro 13 (© SAS Institute Inc. Cary, NC). To determine how much wood management activities reduced woody debris between managed and reduced sites, we used a one-sided Welch's two-sample T-test for unequal variances, given our prediction that wood management reduced CWD. We used similar T-tests to separately compare total, cavity-nesting, and non-cavity-nesting bee abundance and richness between unmanaged and reduced sites. To determine how woody debris impacted bees we explored the relationship between the amount of woody habitat and bee communities with separate linear mixed effect models for several different response variables. In all analyses we included the total volume of woody debris around each bee block (summed across all three

transects) as a fixed factor and the property a site was located on as a random effect to account for multiple sampling sites within properties. Responses included total bee (the total number of all bees netted) abundance and richness, other bee (non-cavity-nesting) abundance and richness, and cavity-nesting bee abundance and richness. In addition, we used coded data on plug abundance and richness from nest blocks to explore cavity-nesting bee composition, using similar linear mixed effect models to explore the relationship between wood availability and cavity-nesting bee nest abundance (the total number of nests combined from blocks and bamboo) and nest richness (the total types of nest plugs). We log (10) transformed all abundance responses and nest plug richness to meet the assumptions of normality.

Results

Woody Debris

In general, BCPOS properties varied widely in the amount of woody debris at each site and in how wood was managed post-flood. In some sites, woody debris was still evident and apparently untouched even three years-post flood. In others, woody debris had been piled to alleviate stream flow or to improve the aesthetics of the riparian areas, and in some instances removed altogether. Subsequently, the volume of CWD measured in transects ranged from zero to 90.82 cubic feet, with an average of 25.83 ± 5.53 cubic feet per site (Figure 3). However, as expected wood management activities resulted in a 50% reduction of CWD on average compared to unmanaged sites ($t_{20.9}$ = 1.7214, p = 0.057, Figure 4). Naturally occurring cavities in wood were relatively rare across CWD transects, especially those greater than 1/16" in diameter. As we found no active bee nests across any of the transected CWD, we did not explore cavity abundance or composition from sampled wood as a factor driving bee communities. However, it should be noted that we did observe a number of important wood habitat features outside of transects. For example, at site 20 located on Bullock, we observed a number of cottonwood snags and recently downed logs that were highly attractive to nesting *Megachile*, where A. Carper counted ~ 100 active nests in just one standing dead cottonwood trunk. Identifying and mapping important nesting habitat features could be an area of future training for BCPOS biologists.

Netted Bee Community

Over 125 person hours of netting we collected a total of 3,662 bees ($\bar{x}$ = 159.2 ± 17.7 bees per site) across 5 families (Andrenidae, Apidae, Colletidae, Halictidae, and Megachilidae) and 33 different genera ($\bar{x}$ = 15.7 ± 0.7 genera per site). Twelve of these genera were dominated by cavity-nesting species ($\bar{x}$ = 6.0 ± 0.4 genera per site) totaling 819 cavity-nesting bees across sites ($\bar{x}$ = 35.6 ± 6.1 per site). The most abundant genera in our netted samples were *Lasioglossum*, making up 24% of all bees, *Apis* (18%), and *Hylaeus* (13%, Table 2). Netting in sites where wood was reduced through managements produced roughly 40% fewer bees than in unmanaged sites ($t_{16.9}$ = -1.86, p = 0.040) although this was driven primarily by other types of bees and not cavity-nesting bees ($t_{18.9}$ = -1.93, p = 0.035 vs. $t_{18.6}$ = -0.59, p = 0.282, respectively, Figure 5a). Bee genus richness at sites with reduced wood did not differ from unmanaged sites, regardless of bee nesting habits (p > 0.278 in all cases, Figure 5b).

Exploring netted bee abundance in relation to the volume of CWD revealed two interesting results. First, we found a significant positive relationship between the volume of

woody debris and the total number of netted bees at each site ($F_{1,16.6} = 5.92$, p = 0.0271, Figure 6a); however, this did not appear to be driven by cavity-nesting bees which showed no significant relationship with wood ($F_{1,19.9} = 0.46$, p = 0.504, Figure 6b), but instead by the number of netted other bees which increased with increasing woody debris ($F_{1,14.5} = 7.23$, p = 0.017, Figure 6b). Secondly, we found no relationships between woody debris and either total bee genus richness, cavity-nesting genus richness, or other genus richness (Table 3), suggesting that other mechanisms likely structure bee genus richness across sites.

Cavity-nesting Bee Community

Trap-nests contained a total of 664 bee nests at the end of the summer, ranging in their material make-up from mud, pebbles, and loose debris to whole leaf pieces, chewed vegetation, and resin (Appendix II). Occupancy rates of trap nests ranged from 17.5-100% (mean occupancy of 57.5%). Excluding wasps, bee occupancy rates ranges from 0 to 97.5% (mean occupancy of 43.7%). We recorded an average of 28.87 ± 4.24 active bee nests per block, representing 2.64 ± 0.22 genera per block on average. Observed genera included *Anthidium*, *Ashmeadiella*, *Heriades*, *Hoplitis*, *Hylaeus*, *Osmia*, and *Megachile*. No block had more than four bee genera represented. We broke *Megachile* nests into two groups: one containing native species, and one containing introduced species – mostly *M. rotundata*. Of these, introduced *Megachile* species (determined by their whole-leaf nest plugs) were the most abundant colonizer, representing 69% of all nests, and present at 74% of all sites (*see* Figure S2). Native *Osmia* was the second most abundant, representing 17.5% of nests, and native *Megachile* were the third most abundant, representing 7.7% of nests.

Interestingly, wood removal did not significantly reduce bee nest abundance ($t_{19.0} = 1.00$, p = 0.835) and in fact was nearly opposite our prediction, tending to increase colonization of bee blocks by some 16% compared to unmanaged sites. Moreover, we found a significant inverse relationship between bee nest abundance and woody debris, suggesting that bee nest abundance in trap nests actually declines with increasing volumes of woody debris ($F_{1,19.8} = 14.34$, p = 0.001, Figure 7). However, similar to the netted bee community, CWD removal had little effect on richness ($t_{16.1} = -.69$, p = 0.249), and we found no relationship between bee nest richness and wood volume ($F_{1,10.2} = 0.41$, p = 0.537).

Discussion

Overall, we found that bee communities on Boulder County Open Spaces along the St. Vrain River are both abundant and diverse, but also highly variable across sites. Our netted samples ranged from less than 50 specimens at one site to almost 400 at another, with diversity ranging from as many as 20 unique genera at some sites to only 8 at one site. Our nest blocks were also highly variable in their success rate, with some not being colonized at all, and some almost completely occupied, with multiple generations of cavity-nesting bees being observed over the season. Moreover, our results suggest that wood management does impact bee communities, and the responses of bees to woody habitat are likely complex and varied. The variability that we found at our sites is supported in the literature. Spatio-temporal variation in bee abundance and diversity has been documented in many different studies, explained by variable weather, floral resources, and landscape composition, and based on species or guild specific variation across habitats (National Research Council 2007, Hoehn et al. 2008, Steckel et

al. 2014). Local bee communities can also vary greatly from year to year. In a study including both temperate and tropical environments, Euglossini bees were found to vary so much in local populations from year to year that the population would have to be sampled for 4 consecutive years to account for the variability (Roubik 2001). That we found significant relationships with relatively coarse measures suggests that further study with our data could help identify even more robust patterns and relationships. As identifications, analyses and research are ongoing, A. Carper will update BCPOS with addendums to this report as needed.

In general, wood management lead to a reduction in both woody debris and overall bee abundance. Interestingly this appeared driven primarily by other types of bees which nested in soil or other areas and not specifically by cavity-nesting bees as we predicted. This was also evident from the positive relationship between woody debris and overall bee abundance and other bee abundance. The associated increase in non-wood nesting species could likely be a result of other habitat variables related to woody debris. For example, given that woody debris is likely related to human disturbance and management (i.e., it is often left in areas with little human disturbance), areas with high amounts of woody debris may also have high amounts of relatively undisturbed soil. Approximately 70% of Boulder County's bee species nest in soil and were no doubt impacted by the flooding that occurred along the St. Vrain Creek. However, such disturbance created a number of habitats which could benefit a number of specialized native bees, including exposed sand bars, scours of bare ground, and vertical banks. We noted several such vertical banks along head cuts at Western Mobile and Keyes, both of which contained nesting aggregations of digger bees (*Anthophora* spp.), masked bees (*Hylaeus* spp.), mining bees (*Andrena* spp.), and sweat bees (*Halictus* spp.). Attention to protecting or enhancing these nesting habitats could prove particularly valuable in managing these specialized ground-nesting species.

While we expected that bee abundance would be positively correlated with CWD volume, we were surprised to find that this trend was driven by CWD's effect on non-cavity nesting genera, while cavity-nesting genera were not significantly affected by volume of CWD. This leads us to believe that there must be some other factors affecting both wood volume and bee abundance. Woody debris' positive effect on local environments is well documented, and many factors could be driving this relationship. Some of the important roles that CWD plays in a riparian environment include nutrient cycling, which could in turn affect floral communities, and affect geomorphic processes, such as the buildup of sediment along rivers that could provide habitat for ground-nesting bees (Harmon et al. 2004, Vazquez et al. 2011). We also consider the possibility that areas with a lower volume of wood could be less disturbed by humans, allowing for a richer bee community to flourish. While identifying and quantifying the floral resources at our sites was beyond the scope of our study, floral resource availability has been shown to have a significant effect on bee communities (Roulston and Goodell 2011, Hanula et al. 2016). This likely makes it difficult to isolate CWD as an independent driver of wild bee communities, and highlights the need for studies measuring both floral and nesting resources. Sharing our data with BCPOS if floral community data are available could help disentangle the relative importance of floral and nesting resources.

Overall, our results do suggest that woody debris may be important for cavity-nesting bees and limit their populations. Cavity-nesting bee abundance tended to increase with increasing volumes of woody debris, though the relationship was not significant. This could be a result of relatively low capture rates compared to non-cavity nesting bees (i.e., more sampling would be necessary to find a relationship), or that cavity-nesting bees are responding to more

specific habitat features, such as floral resources, especially given that many species are fairly specialized on floral hosts. For example, site 16 at Hall Ranch had more than twice as many cavity-nesters as the next most abundant site, but the pattern was driven primarily by a very high abundance of *Hylaeus* that were netted off of flowering choke cherry trees. *Hylaeus* are quite small (some < 4 mm in length) and can likely take advantage of more abundant small cavities. Also, given their small size and associated short foraging range (Greenleaf et al. 2007), they may be more limited by proximity to floral hosts than larger genera such as *Osmia* and *Megachile*. Exploring species- or guild-specific responses within our data should help tease apart the idiosyncratic responses within the community.

While the cavity-nesting bees we found in netted samples were less related to wood volume or it management, we did find strong, inverse relationships between wood and nest block bee abundance. This is intuitive, given that where woody debris is abundant (unmanaged sites), natural cavities are less limiting for cavity-nesting bees and colonization of artificial substrates (in this case trap nests) is relatively low. Conversely, where woody debris is scarce (reduced sites), artificial substrates become very attractive and quickly fill with cavity nesting bees. Other studies have provided evidence that nesting habitat is limiting for cavity nesting species and that it can be reflected through artificial nest colonization. For example, older orchard meadows with aging fruit trees in Northern Germany had a higher abundance and diversity of cavity-nesting bees and wasps than open grasslands, presumably due to the availability of wood habitat, since there were little differences in floral communities (Tscharntke et al. 1998). Many of the BCPOS properties we sampled included feral apple and pear trees, as well as native choke cherries and plums which are particularly attractive to early season Megachilids such as *Osmia.* These trees often have dead branches which could provide suitable habitat for nesting bees and in close proximity to their floral resources. Closer inspection of such areas could help to determine their overall value to bees in those sites. Overall, while we were initially surprised by the inverse relationship between nest abundance in our monitoring blocks and woody debris, we subsequently found it promising for two reasons. First, it implies that woody debris is creating important habitat for cavity-nesting bees and does have conservation value. Second, in areas where woody debris is lacking or must be removed, the addition of artificial habitat (i.e., nest blocks, bamboo, external wood, etc.) can be an effective conservation tool to support wild cavity-nesting bees.

That we had such high colonization rates of blocks in sites with little wood also strongly suggests bees were limited for nests in those sites and artificial habitat itself has been demonstrated to benefit cavity-nesting bees. Another study in Germany found that experimentally enhancing nest site availability over four years resulted in a nearly 35 fold increase of local populations sizes of *Osmia rufa* brood cells (Steffan-Dewenter and Schiele 2008). This suggests that cavities are extremely limiting to population growth, especially for larger bee species, given that not all cavities are equal. For example, in a study in Sweden, Westerfelt et al. found that only approximately 1.8% of natural cavities surveyed were colonized by bees or wasps, compared to nearly 32% of the artificial cavities they provided (Westerfelt et al. 2015). This pattern is strikingly similar to what we observed in our sites. This was presumable because of huge variation in the size of natural cavities, with most being too small, or the suitability of wood (i.e., decay stage, moisture content, etc.) not appropriate for nesting bees. Therefore, leaving debris of many different tree species and size classes could provide the maximum potential habitat for a diverse cavity nesting bee fauna.

It is also important to note that cavity-nesting bees are intricately linked with the insects that make their cavities, namely beetles, and that dynamics in beetle communities over space and time could be driving cavity-nesting bee communities. Few studies have addressed such non-trophic linkages in bee communities and just one to our knowledge pertains specifically to cavity-nesting bees. Sydenham et al. explored associations between wood boring beetles and bees of different sizes in forests in Norway. They found that the abundance of large wood boring beetles was the single most important factor driving cavity-nesting bee abundance and species richness, suggesting that identifying and managing non-trophic facilitative interactions may be of high importance for restoration and conservation (Sydenham et al. 2016). That is, managing for floral resources or even woody debris alone may not be sufficient for promoting cavity-nesting bees, if the strategies to also promote large beetles that excavate cavities aren't also implemented. Given the scarcity of large natural cavities in our study, it is likely that suitable wood nesting substrates are rare and probably concentrated spatially across the landscape. Exploring the abundance and diversity of beetle and natural cavity availability could increase our understanding of the role of nest-site limitation in cavity-nesting bees. These and other future analyses could help disentangle the ecological phenomenon driving these patterns. Ultimately, ecosystem-scale management is probably one of the strongest ways to insure community linkages.

In summary, given recent concern over native pollinators, this study adds to a growing body of literature on factors driving native pollinator community dynamics and produces some management recommendations for best practices in terms of woody debris management for native pollinators. Clearly, woody debris contributes significantly to the health of native bee communities. Moreover, the strongest effect of woody debris on bee communities goes beyond what it provides for nesting habitat for cavity-nesters, and likely has positive indirect effects on the entire bee community. We believe our data provide a strong case against its removal in riparian ecosystems whenever possible. In areas where it must be removed, while bee blocks cannot replace the role that CWD plays for non-cavity nesters, we have demonstrated that many native cavity nesting bees will utilize artificial nesting blocks. We have also started to explore the most effective type of trap nest to use to serve native bee conservation. We hope that our data can be utilized by land managers as they make decisions about woody debris management and by bee researchers as they continue to gauge the status of native bees and how to best conserve them.

Table 1. Locations of trap nests and categorization of wood management activities.

Block	Latitude	Longitude	Property	Treatment	Wood Debris Management
169013	40.20176327	-105.29830199	Hall Ranch 2	Control	Unmanaged
169014	40.20395095	-105.29405622	Hall Ranch 2	Control	Unmanaged
169015	40.20661320	-105.29336421	Hall Ranch 2	Reduced	Removed debris from site
169016	40.20963840	-105.28752512	Hall Ranch	Control	Unmanaged
169017	40.20967185	-105.28194202	Hall Ranch	Control	Unmanaged
169018	40.21029906	-105.27949140	Hall Ranch	Reduced	Debris piled and removed from new flow path
169019	40.21548788	-105.27550556	Hall Ranch	Control	Unmanaged
169020	40.21118738	-105.24162750	Bullock	Control	Unmanaged
169021	40.20913591	-105.24103289	Western Mobile	Control	Unmanaged
169022	40.21110171	-105.23720236	Wallace	Reduced	Removed debris from the stream bank
169023	40.20695678	-105.22637528	Montgomery	Control	Unmanaged
169024	40.20603167	-105.22408241	Western Mobile	Reduced	Removed debris from the stream bank
169025	40.20374777	-105.21992290	Western Mobile	Reduced	Debris removed from the stream channel
169026	40.19899414	-105.21706970	Western Mobile	Control	Unmanaged
169027	40.19825703	-105.21507313	Braly	Control	Unmanaged
169028	40.19489706	-105.20741240	Ramey	Reduced	Debris was removed
169029	40.18818257	-105.19617939	Gage	Reduced	Irrigation ditch manager removed debris
169030	40.18775669	-105.19255120	Gage	Reduced	Debris piled
169031	40.18138451	-105.18567553	Pella Crossing	Control	Unmanaged
169032	40.17935693	-105.18295325	Pella Crossing	Control	Unmanaged
169033	40.17844096	-105.18110546	Pella Crossing	Control	Unmanaged
169034	40.17777770	-105.17530343	Golden-Fredstrom	Reduced	Debris removed or perhaps piled elsewhere
169035	40.17716280	-105.17113879	Golden-Fredstrom	Control	Unmanaged
169036	40.15160621	-105.06947645	Keyes	Control	Unmanaged
169037	40.15208691	-105.06012443	Keyes	Reduced	Debris removed form field

Table 2. Genera captured through netting, their abundance, and percentage of the overall community.

Family	Genus	Total	Percent
Andrenidae	*Andrena*	222	6.1
	Calliopsis	1	0
	Ceratina*	65	1.8
	Nomada	29	0.8
	Perdita	89	2.4
	Pseudopanurgus	3	0.1
Apidae	*Anthophora*	9	0.2
	Apis	669	18.3
	Bombus	292	8
	Melissodes	111	3
	Peponapis	1	0
	Svastra	7	0.2
	Triepeolus	4	0.1
Colletidae	*Colletes*	24	0.7
	Hylaeus*	495	13.4
Halictidae	*Agapostemon*	21	0.6
	Augochlorella	23	0.6
	Augochloropsis	5	0.1
	Dufourea	7	0.2
	Halictus	414	11.3
	Lasioglossum	880	24
	Sphecodes	32	0.9
Megachilidae	*Anthidium**	4	0.1
	Ashmeadiella*	6	0.2
	Coelioxys*	13	0.4
	Dianthidium*	11	0.3
	Heriades*	27	0.7
	Hoplitis*	32	0.9
	Lithurgopsis*	13	0.4

Megachile*	119	3.2
Osmia*	29	0.8
Stelis*	5	0.1
Grand Total	3,662	100

*indicates cavity-nesting genus

Table 3. Effect tests for the volume of woody debris

Response	Num DF	Den DF	F-ratio	p-value	
Netted Abundance					
log10(total)	1	16.57	5.920	0.027	*
log10(other)	1	14.45	7.230	0.017	*
log10(cavity-nesting)	1	19.98	0.460	0.504	
Netted Genus Richness					
total	1	18.64	0.550	0.468	
other	1	18.82	1.830	0.192	
cavity-nesting	1	19.22	0.004	0.948	
Trap Nests					
log10(nest abundance)	1	19.83	14.340	0.001	***
log10(nest richness)	1	10.24	0.410	0.537	

Figure 1.
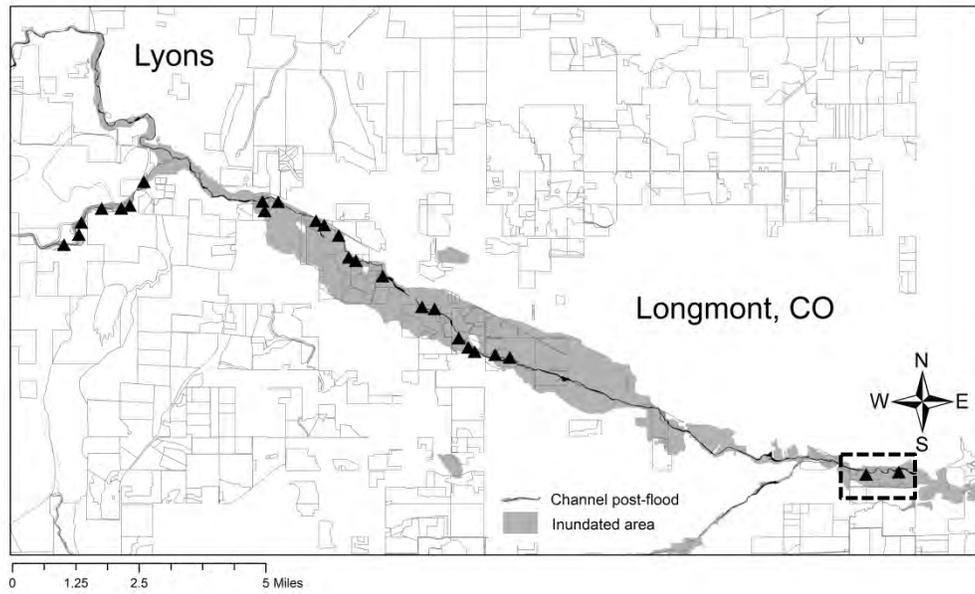
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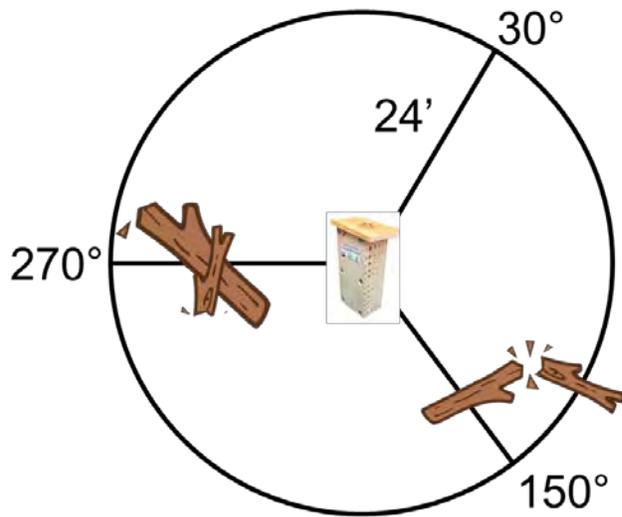
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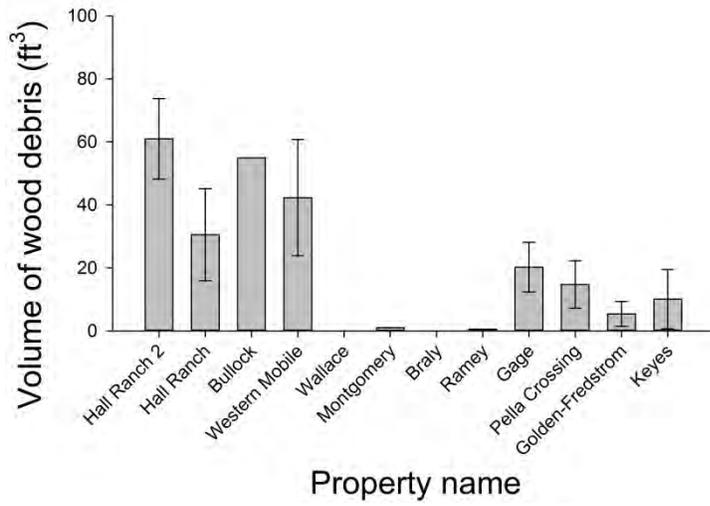
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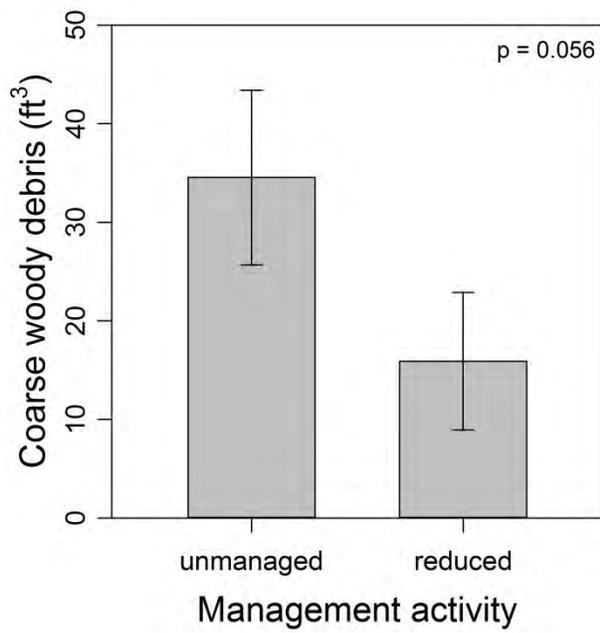
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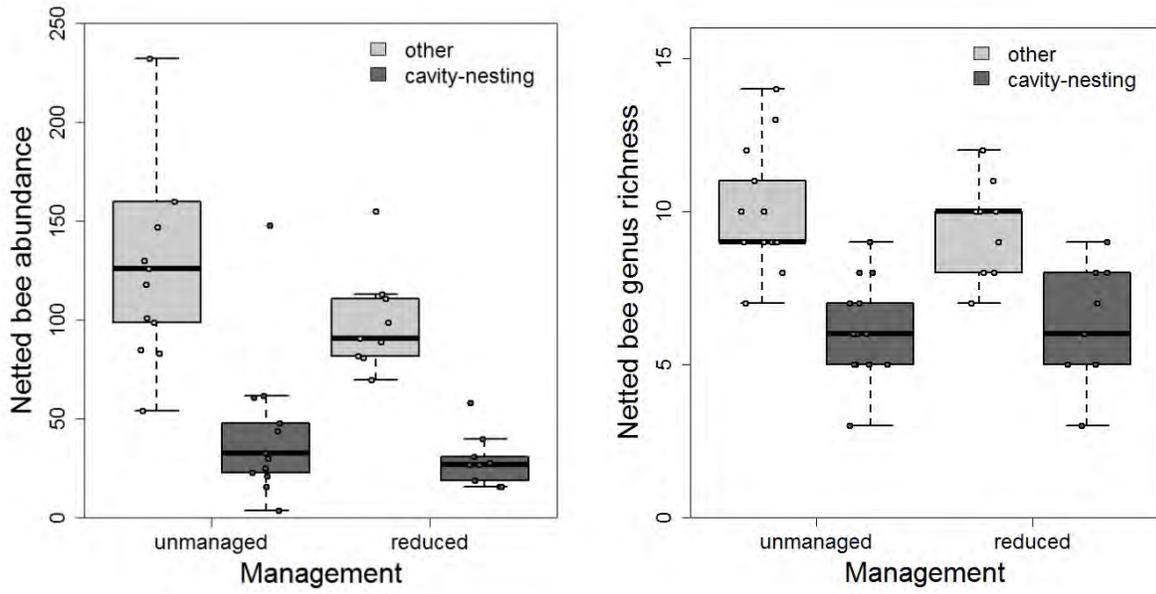
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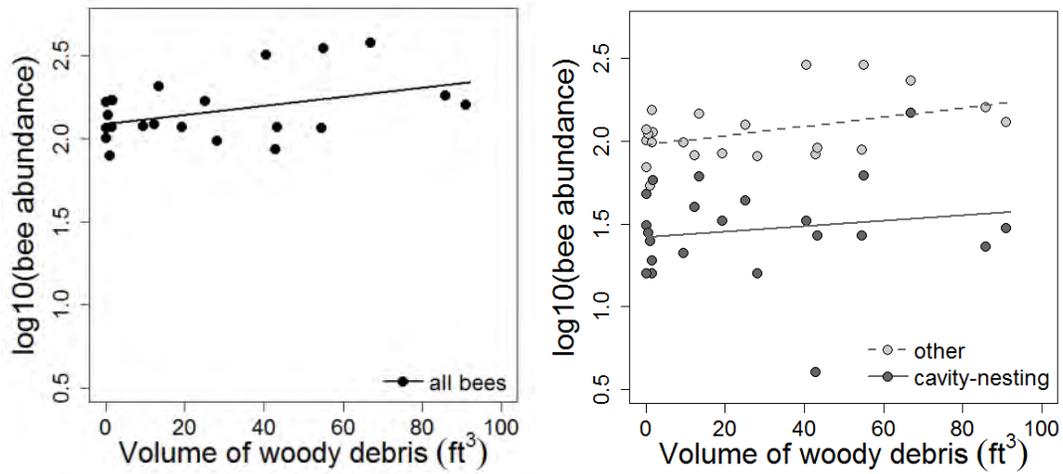
Figure 7.
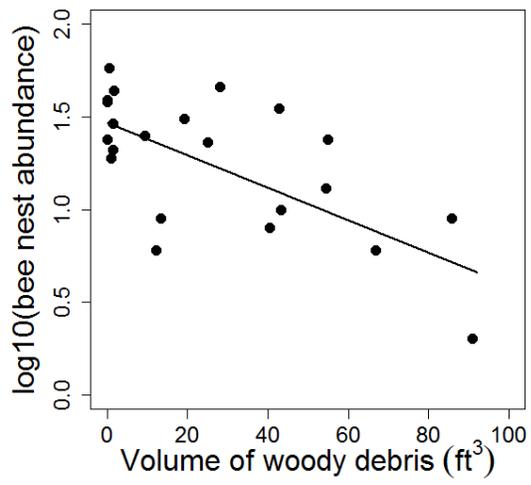
Figure Legends

Figure 1. Sampling sites spanned ~20 miles of the St. Vrain Creek west of Lyons east past Longmont, CO. Two sites were isolated from others, being east of Longmont, and were excluded from statistical analyses. Outlines represent current Boulder County Parks and Open Space properties.

Figure 2. Woody debris was sampled using three 24-foot line intercept transects oriented and 30, 150, and 270°, respectively.

Figure 3. BCPOS properties varied in the total amount of woody debris. Error bars represent standard errors from properties with more than one sampling location. Bars without error bars had only one sampling location.

Figure 4. Wood management activities across managed sites resulted in an ~50% reduction in coarse woody debris on average compared to unmanaged sites.

Figure 5. Sites where wood was reduced through management had ~40 fewer bees than in unmanaged sites **a)** although this was driven primarily by non-cavity nesting species; **b)** Bee genus richness at sites with reduced wood did not differ from unmanaged sites.

Figure 6. We found a significant positive relationship between the total volume of woody debris and **a)** the total number of bees captured in netting surveys, although the relationship was mostly driven by **b)** the number of non-cavity-nesting bees. Points represent individual sampling locations. Solid and hashed lines represent the predicted values and standard deviation from the fitted model.

Figure 7. We found a significant negative relationship between the total volume of woody debris at each site and **a)** the total number of nests recorded in bee blocks and bamboo. Coded data on bee nests from bee blocks **b)** indicated a similar negative relationship between bee nest abundance and woody debris. Points represent individual sampling locations. Solid and hashed lines represent the predicted values and standard deviation from the fitted model.

Appendix I. Supplemental Data and Figures

Table S1. Locations of 25 sites used to survey for wild bees using wooden and bamboo trap nests. Block # refers to a unique catalogue number for wooden trap nests. Bamboo trap nests were mounted within 5-10 meters of the recorded location of each wooden trap nest.

Property	Block #	Latitude	Longitude	Elevation (m)
Hall Ranch 2	169013	40.20176	-105.29830	1659
Hall Ranch 2	169014	40.20395	-105.29406	1681
Hall Ranch 2	169015	40.20661	-105.29336	1676
Hall Ranch	169016	40.20964	-105.28753	1665
Hall Ranch	169017	40.20967	-105.28194	1658
Hall Ranch	169018	40.21030	-105.27949	1655
Hall Ranch	169019	40.21549	-105.27551	1645
Bullock	169020	40.21119	-105.24163	1605
Western Mobile	169021	40.20914	-105.24103	1602
Wallace	169022	40.21110	-105.23720	1601
Montgomery	169023	40.20696	-105.22638	1601
Western Mobile	169024	40.20603	-105.22408	1598
Western Mobile	169025	40.20375	-105.21992	1589
Western Mobile	169026	40.19899	-105.21707	1578
Braly	169027	40.19826	-105.21507	1574
Ramey	169028	40.19490	-105.20741	1571
Gage	169029	40.18818	-105.19618	1566
Gage	169030	40.18776	-105.19255	1559
Pella Crossing	169031	40.18138	-105.18568	1552
Pella Crossing	169032	40.17936	-105.18295	1561
Pella Crossing	169033	40.17844	-105.18111	1550
Golden-Fredstrom	169034	40.17778	-105.17530	1537
Golden-Fredstrom	169035	40.17716	-105.17114	1523
Keyes	169036	40.15161	-105.06948	1491
Keyes	169037	40.15209	-105.06012	1488

Table S2. Species and morphodeterminations of bees by property.

Braly	Bullock	Gage
Andrenidae	**Andrenidae**	**Andrenidae**
Andrena spp.	*Andrena spp.*	*Andrena spp.*
Nomada spp.	*Ceratina spp.*	*Ceratina spp.*
Perdita spp.	*Nomada spp.*	*Nomada spp.*
Apidae	**Apidae**	*Perdita spp.*
Apis mellifera	*Apis mellifera*	**Apidae**
Bombus appositus	*Bombus appositus*	*Anthophora spp.*
Bombus fervidus	*Bombus fervidus*	*Apis mellifera*
Bombus griseocollis	*Bombus griseocollis*	*Bombus appositus*
Bombus huntii	*Bombus huntii*	*Bombus bifarius*
Bombus nevadensis	*Bombus pennsylvanicus*	*Bombus fervidus*
Melissodes spp.	*Melissodes spp.*	*Bombus griseocollis*
Colletidae	*Svastra obliqua*	*Bombus huntii*
Colletes spp.	*Triepeolus spp.*	*Bombus nevadensis*
Hylaeus leptocephalus	**Colletidae**	*Bombus occidentalis*
Hylaeus spp.	*Hylaeus leptocephalus*	*Melissodes spp.*
Halictidae	*Hylaeus spp.*	**Colletidae**
Agapostemon spp.	*Hylaeus wootoni*	*Colletes spp.*
Augochlorella aurata	**Halictidae**	*Hylaeus affinis*
Halictus ligatus	*Agapostemon spp.*	*Hylaeus leptocephalus*
Halictus spp.	*Augochlorella aurata*	*Hylaeus spp.*
Lasioglossum (Dialictus) spp.	*Halictus ligatus*	**Halictidae**
Lasioglossum spp.	*Halictus spp.*	*Augochlorella aurata*
Megachilidae	*Lasioglossum (Dialictus) spp.*	*Halictus ligatus*
Hoplitis producta	*Lasioglossum spp.*	*Halictus spp.*
Megachile montivaga	*Sphecodes spp.*	*Lasioglossum (Dialictus) spp.*
Megachile parallela	**Megachilidae**	*Lasioglossum spp.*
Megachile perihirta	*Ashmeadiella bucconis*	*Sphecodes spp.*
Megachile pugnata	*Heriades carinata*	**Megachilidae**
Megachile rotundata	*Hoplitis fulgida*	*Anthidium porterae*
Osmia sp.7	*Hoplitis pilosifrons*	*Coelioxys sayi*
Stelis sp.2	*Megachile brevis*	*Dianthidium parvum*
	Megachile fidelis	*Dianthidium ulkei*
	Megachile perihirta	*Heriades variolosa*
	Megachile pugnata	*Hoplitis fulgida*
	Megachile rotundata	*Hoplitis producta*
	Megachile subexilis	*Hoplitis spp.oliata*
	Osmia sp.10	*Megachile centuncularis*
	Osmia sp.3	*Megachile frigida*
	Stelis sp.2	*Megachile inimica*
		Megachile montivaga
		Megachile perihirta
		Megachile rotundata
		Megachile subexilis
		Osmia sp.10

Golden-Fredstrom	Hall Ranch	Hall Ranch 2
Andrenidae	**Andrenidae**	**Andrenidae**
Andrena spp.	*Andrena spp.*	*Andrena spp.*
Ceratina spp.	*Ceratina spp.*	*Ceratina spp.*
Perdita spp.	*Nomada spp.*	*Nomada spp.*
Pseudopanurgus spp.	*Perdita spp.*	*Perdita spp.*
Apidae	**Apidae**	**Apidae**
Apis mellifera	*Apis mellifera*	*Anthophora spp.*
Bombus appositus	*Bombus appositus*	*Apis mellifera*
Bombus centralis	*Bombus centralis*	*Bombus appositus*
Bombus huntii	*Bombus fervidus*	*Bombus centralis*
Bombus spp.	*Bombus griseocollis*	*Bombus griseocollis*
Bombus nevadensis	*Bombus huntii*	*Bombus huntii*
Bombus pennsylvanicus	*Bombus nevadensis*	*Bombus melanopygos*
Bombus rufocinctus	*Bombus pennsylvanicus*	*Bombus spp.*
Melissodes bimaculata	*Bombus rufocinctus*	*Bombus nevadensis*
Melissodes spp.	*Melissodes spp.*	*Triepeolus spp.*
Peponapis pruinosa	*Svastra obliqua*	**Colletidae**
Colletidae	**Colletidae**	*Colletes spp.*
Hylaeus leptocephalus	*Colletes spp.*	*Hylaeus coloradensis*
Hylaeus spp.	*Hylaeus (paraprosopis) spp.*	*Hylaeus episcopalis*
Halictidae	*Hylaeus affinis*	*Hylaeus leptocephalus*
Agapostemon spp.	*Hylaeus coloradensis*	*Hylaeus spp.*
Augochlorella aurata	*Hylaeus episcopalis*	*Hylaeus wootoni*
Halictus ligatus	*Hylaeus leptocephalus*	**Halictidae**
Halictus spp.	*Hylaeus spp.*	*Augochlorella aurata*
Lasioglossum (Dialictus) spp.	*Hylaeus wootoni*	*Augochloropsis spp.*
Lasioglossum spp.	**Halictidae**	*Halictus ligatus*
Sphecodes spp.	*Agapostemon spp.*	*Halictus spp.*
Megachilidae	*Augochlorella aurata*	*Lasioglossum (Dialictus) spp.*
Anthidium oblongatum	*Augochloropsis spp.*	*Lasioglossum spp.*
Coelioxys sayi	*Halictus ligatus*	**Megachilidae**
Dianthidium pudicum	*Halictus spp.*	*Ashmeadiella bucconis*
Heriades variolosa	*Lasioglossum (Dialictus) spp.*	*Coelioxys apacheorum*
Hoplitis producta	*Lasioglossum spp.*	*Heriades carinata*
Megachile brevis	*Sphecodes spp.*	*Lithurgopsis apicalis*
Megachile centuncularis	**Megachilidae**	*Megachile fidelis*
Megachile frigida	*Coelioxys apacheorum*	*Megachile inimica*
Megachile mendica	*Coelioxys sp.1*	*Megachile montivaga*
Megachile perihirta	*Heriades carinata*	*Megachile perihirta*
Megachile relativa	*Hoplitis pilosifrons*	*Megachile pugnata*
Megachile rotundata	*Lithurgopsis apicalis*	*Megachile rotundata*
	Megachile montivaga	*Osmia sp.4*
	Megachile perihirta	*Sphecodes spp.*
	Megachile pugnata	*Stelis rudbeckiarum*
	Megachile rotundata	
	Megachile snowii	
	Osmia sp.10	
	Osmia sp.6	
	Osmia sp.8	

Keyes	Montgomery	Pella Crossing
Andrenidae	**Andrenidae**	**Andrenidae**
Andrena spp.	*Andrena spp.*	*Andrena spp.*
Ceratina spp.	*Ceratina spp.*	*Ceratina spp.*
Nomada spp.	*Nomada spp.*	*Nomada spp.*
Perdita spp.	**Apidae**	**Apidae**
Apidae	*Apis mellifera*	*Anthophora spp.*
Apis mellifera	*Bombus fervidus*	*Apis mellifera*
Bombus griseocollis	*Bombus griseocollis*	*Bombus appositus*
Bombus huntii	*Melissodes spp.*	*Bombus bifarius*
Bombus nevadensis	**Colletidae**	*Bombus centralis*
Bombus pennsylvanicus	*Hylaeus spp.*	*Bombus fervidus*
Melissodes bimaculata	**Halictidae**	*Bombus griseocollis*
Melissodes spp.	*Agapostemon spp.*	*Bombus huntii*
Svastra obliqua	*Halictus ligatus*	*Bombus nevadensis*
Triepeolus spp.	*Halictus spp.*	*Bombus pennsylvanicus*
Colletidae	*Lasioglossum (Dialictus) spp.*	*Melissodes bimaculata*
Colletes spp.	*Lasioglossum spp.*	*Melissodes spp.*
Hylaeus (paraprosopis) spp.	*Sphecodes spp.*	**Colletidae**
Hylaeus affinis	**Megachilidae**	*Colletes spp.*
Hylaeus leptocephalus	*Heriades variolosa*	*Hylaeus affinis*
Hylaeus spp.	*Hoplitis pilosifrons*	*Hylaeus modestus*
Halictidae	*Hoplitis producta*	*Hylaeus spp.*
Agapostemon spp.	*Megachile mendica*	**Halictidae**
Halictus ligatus	*Megachile perihirta*	*Dufourea spp.*
Halictus spp.		*Halictus ligatus*
Lasioglossum (Dialictus) spp.		*Halictus spp.*
Lasioglossum spp.		*Lasioglossum spp.*
Sphecodes spp.		*Sphecodes spp.*
Megachilidae		**Megachilidae**
Heriades carinata		*Coelioxys apacheorum*
Megachile centuncularis		*Coelioxys sayi*
Megachile montivaga		*Hoplitis producta*
Megachile perihirta		*Hoplitis spp.oliata*
Megachile pugnata		*Lithurgopsis apicalis*
Megachile rotundata		*Megachile centuncularis*
Osmia sp.3		*Megachile inimica*
Sphecodes spp.		*Megachile pugnata*
		Megachile relativa
		Megachile rotundata
		Megachile subexilis
		Osmia lignaria
		Osmia sp.1
		Osmia sp.10
		Osmia sp.5

Ramey	Wallace	Western Mobile
Andrenidae	**Andrenidae**	**Andrenidae**
Andrena spp.	*Andrena spp.*	*Andrena spp.*
Ceratina spp.	*Nomada spp.*	*Calliopsis spp.*
Nomada spp.	**Apidae**	*Ceratina spp.*
Apidae	*Apis mellifera*	*Nomada spp.*
Anthophora spp.	*Bombus appositus*	*Perdita spp.*
Apis mellifera	*Bombus fervidus*	*Pseudopanurgus spp.*
Bombus fervidus	*Bombus griseocollis*	**Apidae**
Bombus huntii	*Bombus huntii*	*Anthophora spp.*
Bombus pennsylvanicus	*Bombus nevadensis*	*Apis mellifera*
Melissodes spp.	*Melissodes bimaculata*	*Bombus appositus*
Colletidae	*Melissodes spp.*	*Bombus centralis*
Colletes spp.	**Colletidae**	*Bombus fervidus*
Hylaeus leptocephalus	*Hylaeus spp.*	*Bombus griseocollis*
Hylaeus spp.	*Hylaeus wootoni*	*Bombus huntii*
Halictidae	**Halictidae**	*Bombus nevadensis*
Agapostemon spp.	*Agapostemon spp.*	*Bombus pennsylvanicus*
Halictus ligatus	*Halictus spp.*	*Bombus rufocinctus*
Halictus spp.	*Lasioglossum (Dialictus) spp.*	*Melissodes spp.*
Lasioglossum (Dialictus) spp.	*Lasioglossum spp.*	*Triepeolus spp.*
Lasioglossum spp.	**Megachilidae**	**Colletidae**
Megachilidae	*Dianthidium ulkei*	*Hylaeus leptocephalus*
Coelioxys sp.2	*Heriades variolosa*	*Hylaeus spp.*
Dianthidium ulkei	*Lithurgopsis apicalis*	*Hylaeus wootoni*
Hoplitis fulgida	*Megachile fidelis*	**Halictidae**
Hoplitis producta	*Megachile frigida*	*Agapostemon spp.*
Hoplitis spoliata	*Megachile perihirta*	*Augochlorella aurata*
Lithurgopsis apicalis	*Osmia sp.10*	*Dufourea spp.*
Megachile brevis	*Osmia sp.3*	*Halictus ligatus*
Megachile centuncularis		*Halictus spp.*
Megachile montivaga		*Lasioglossum (Dialictus) spp.*
Osmia sp.10		*Lasioglossum (Dialictus) tegulare*
Osmia sp.9		*Lasioglossum spp.*
		Sphecodes spp.
		Megachilidae
		Anthidium oblongatum
		Ashmeadiella bucconis
		Coelioxys sayi
		Dianthidium pudicum
		Hoplitis fulgida
		Hoplitis pilosifrons
		Hoplitis producta
		Lithurgopsis apicalis
		Megachile brevis
		Megachile centuncularis
		Megachile fidelis
		Megachile frigida
		Megachile inimica
		Megachile lippiae
		Megachile montivaga
		Megachile nivalis
		Megachile perihirta
		Megachile pugnata
		Megachile relativa
		Megachile rotundata

Megachile subexilis
Osmia sp.1
Osmia sp.10
Osmia sp.2
Stelis sp.2

Figure S1. Most native cavity-nesting bees are secondary cavity-nesters, using holes already made by other insects such as carpenter ants (a) and large beetles. A handful of bees, such as this *Megachile* sp (b), are capable of excavating cavities in soft or decaying wood.
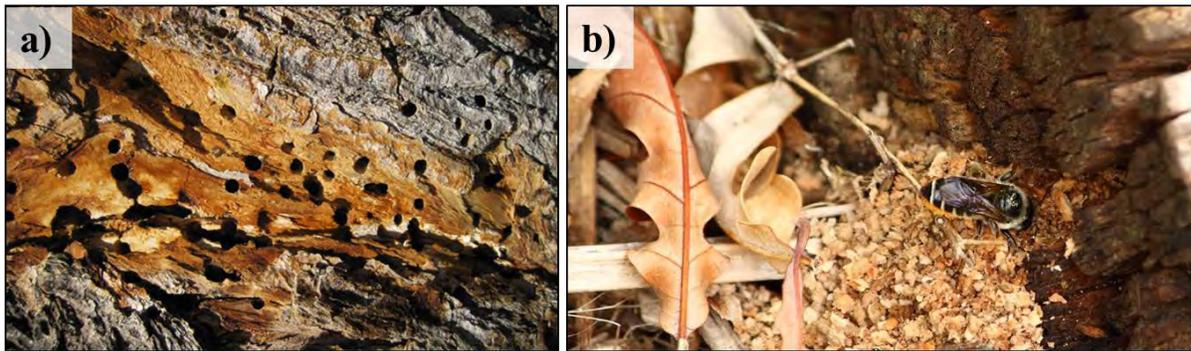
Figure S2. An example composite time lapse photo sequence shows a predated buprestid beetle emerging from its cavity, followed by the colonization and completion of a leaf-cutter bee nest (*Megachile* sp.).

Figure S3. Both Douglas fir bee (a) and bamboo blocks (b) consisted of 40 cavities, 5 each of 1/16", 1/8", 3/16", 1/4", 5/16", 3/8", 7/16", and 1/2". Two different species of cavity-nesting bees: a mason bee using mud to cap cells (c), and a leaf-cutter bee carrying leaf pieces to wrap provisions and cap its nest (d).
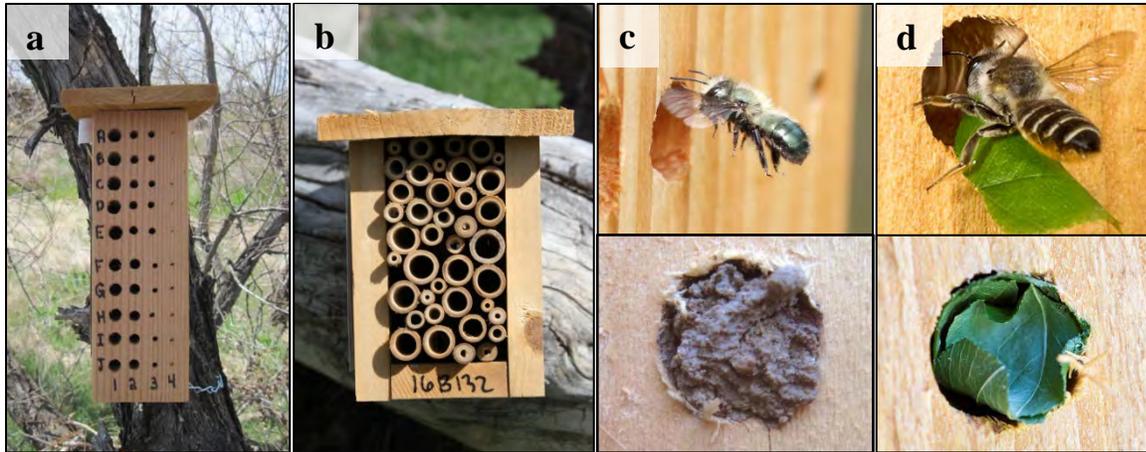
Appendix II. Notes on trap nest efficacy.

Given that we used two separate block designs, we also separated captures by block substrate (bamboo vs. wood), to explore the efficacy of different methods. In addition to bees, we also captured many wasps and found the community of wasps in trap nests (199 nests) dominated by grass carrying wasps (*Isodontia* spp.) making up 42% of nests, potter wasps (Eumeninae) at 37%, and *Solierella* spp. wasps (Crabronidae) at 10% of nests. In terms of bees, bamboo blocks contained a total of 211 nests, representing 31.8% of all nests, compared to the wood blocks which contained a total of 453 nests, or 68.2% of all nests. The wood blocks were more attractive to non-natives than the bamboo: 75.9% of wood block nest were introduced *Megachile rotundata*, while only 54% of bamboo block nests were. In fact, 75.1% of all introduced *Megachile rotundata* nests were in wood blocks. *Osmia* species showed a slight preference for wood nesting blocks (43.1% in bamboo, and 56.9% in wood), however they made up a larger proportion of nests in bamboo (23.7%) than nests in wood (14.6%). Native *Megachile* showed a slight preference for bamboo nesting blocks (58.8% in bamboo, and 41.2% in wood), but also represented a larger portion of total bamboo nests (14.2%) than wood nests (4.6%). *Ashmeadiella* and *Heriades* were the rarest colonizers, making only 3 and 1 nest, respectively. The genera *Ceratina, Coelioxys, Dianthidium, Lithurgopsis, and Stelis* were present in netted samples, but not in any of our nest blocks. Overall, while wooden blocks only had 3% less native bee nests than bamboo on average (t = -0.13, p = 0.45), the proportion of native bee nests within wood blocks was 30% lower than in bamboo (t = -1.81, p = 0.045), suggesting that while both block types supported the same number of native cavity nesters, wooden blocks were disproportionally used by introduced species.

The effectiveness of nesting blocks for both monitoring and conserving wild bees has been variable across studies of different bee species, habitats, and study types. While one study in California found a significant relationship between nest block density and distribution and the reproductive success of the *Osmia lignaria* bees using them (Artz et al. 2013), others question the ability of the blocks to accurately represent local cavity-nesting bee communities, and note the high rate of parasitism and colonization by non-natives or wasps as potential pitfalls (Cane et al. 2007, Gardner and Spivak 2014, MacIvor and Packer 2015). Our results support the contention that trap nests need to be further studied and modified for maximum effectiveness as both monitoring and conservation tools. As monitoring tools, the blocks were moderately effective. As has been noted in other studies, some cavity nesting species did not utilize the blocks at all, and in general the blocks represented only a fraction of the actual cavity nesting bee richness at each site. We found that our netting samples contained on average 4 more genera of cavity nesting bees than did our nest blocks, indicating that much of the cavity nesting diversity present at a site may not be represented in nest blocks. We hypothesize that rarer and native cavity-nesting genera may have been outcompeted for nest-block habitat by the highly abundant introduced *Megachile rotundata*, which dominated our nest-blocks, constructing almost 70% of the total nests. This effect is an important consideration when assessing the conservation value of nesting blocks.

The difference in proportion of each type of block that was used by different genera lead us to believe that bamboo nesting blocks would be more effective than wood for monitoring and conserving native bee genera. Although many of the genera of native bees nested preferentially in the wood, the proportion of the bamboo occupied by native bees was much higher than that of wood. Since the proportion of wood that was occupied by non-natives was much higher than that

of bamboo, we believe that intensive colonization by introduced *Megachile* species could have a negative effect on colonization by natives, and that this problem is stronger in wood blocks. We believe that more research needs to be done to determine the differences in colonization of artificial nesting substrate in order to develop the most effective way to monitor, conserve, and manage native bees.

Figure S4. While there was no difference in **a)** total numbers of nests between bamboo and wooden nest blocks, **b)** bamboo nest blocks had 42% higher proportion of native bee nests compared to wooden blocks.
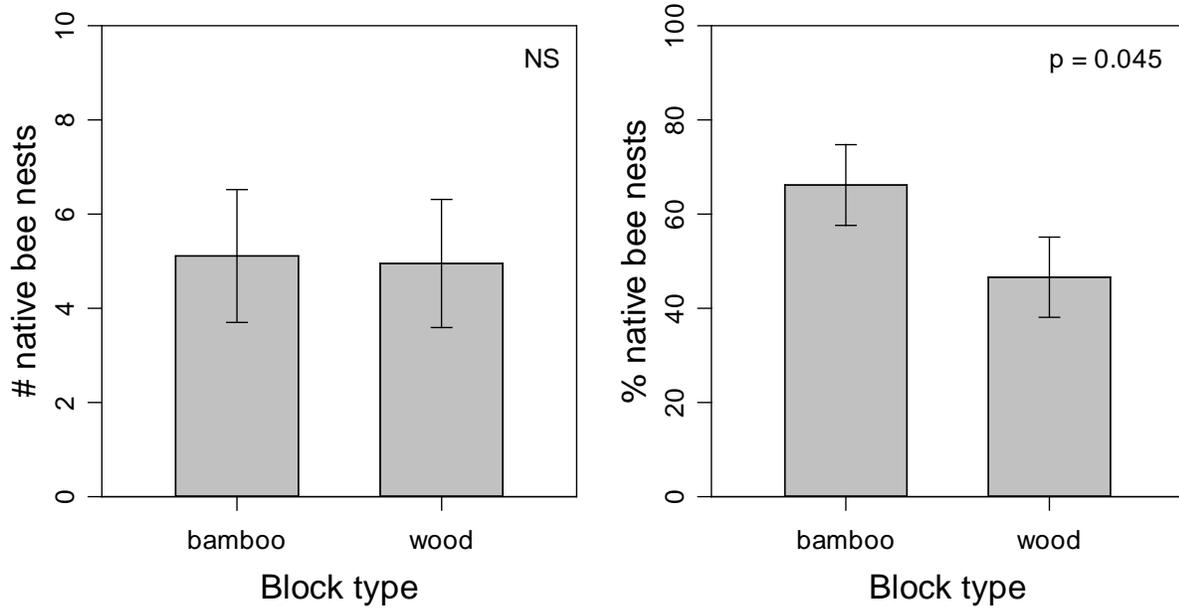
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