

**THE EFFECT OF FIRE DISTURBANCE ON BEE COMMUNITY COMPOSITION IN
OAK SAVANNAH HABITAT IN SOUTHERN ONTARIO, CANADA**

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Abstract

Determining how bee communities respond to environmental disturbance is crucial for ensuring that the pollination service that bees provide is sustained. Studies have reported that bee communities respond to environmental disturbance; however they have not experimentally tested whether environmental disturbances are important for maintaining bee diversity. Unlike other studies of the impact of fire upon bees, this thesis is based upon experimental tests. I investigate whether fire disturbance plays a significant role in maintaining bee community diversity and composition, and how individual species occupy various ages of post-burn habitat. Freshly burned (< 4 years since fire), intermediate burn (5-10 years since fire), mature burn (15-20 years since fire) and control (no fire) plots were used in two oak savannah remnants in Southern Ontario. Results show fire to be an important environmental disturbance for maintaining bee diversity in the temporal sense, as bee diversity was at its highest in intermediate age burns. Bee diversity increased significantly immediately post fire in fresh habitat but high diversity was short lived whereas mature site bee diversity declined over time. Rank abundance plots and community composition analyses revealed bee communities differed in species composition among replicates of the same age since fire within localities and over time. Bee communities within localities showed similarities in composition. Functional nesting guilds examined were solitary and social ground nesters, cavity nesters, *Bombus* spp. and cleptoparasites. The relative proportional abundance of species within functional nesting guilds also varied over time and burn site. An examination into how bee species within functional guilds occupy burned habitat indicated that bee species of the same functional guild occupy burned habitat differently. Occupancy modeling of the 12 most common bee species suggests the need for more thorough

assessments of the ecologies of individual species in order to fully determine how bee communities respond to environmental disturbances.

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Statement of authorship

By submitting this dissertation for partial fulfillment for the degree of doctor of philosophy, I, Alana Pindar acknowledge that it is entirely my own work that was conducted while a graduate student under the supervision of Dr. Laurence Packer in the department of biology at York University. Chapters 2- 4 contain the word 'we' as both names were put on the manuscript for the submission process. I completed the work and wrote the original manuscripts while Dr. Packer was the principle investigator and offered technical suggestions in writing each manuscript.

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Chapter 1- Introduction

1.1 The importance of Bees and quantifying changes in bee communities

Ecosystem services are ecological processes that are essential for human well being that are provided by nature for free (Daily, 1997). These services include pollination, seed dispersal, water purification, and pest control (Luck *et al.*, 2003). When the biodiversity of an ecosystem is in jeopardy, so too are the ecosystem services which it provides. Presently some of these services have been threatened because of the scale of anthropogenic activities (Díaz *et al.*, 2006). For example, recently it has been documented that the world's fresh water supply is threatened by human disturbances (Vorosmarty *et al.*, 2010). Furthermore, it has been estimated that over the next several decades millions of plant and animal species will go extinct due to the way we exploit their ecosystems (Cardinale *et al.*, 2012; Hughes *et al.*, 2002; Tschamntke *et al.*, 2012). The Convention on Biological Diversity has declared the current decade (2011-2020) the 'Decade of Biodiversity' (CBD, 2013) with hopes of reducing both the current rate of biodiversity loss and pressures on biodiversity by 2020 (CBD, 2013). The target is bold, but essential in order to conserve the ecosystem services that biodiversity provides.

Pollination services provided by bee communities are one of the most crucial ecosystem services (Kremen *et al.*, 2007). Pollination by bees in agro-ecosystems in North America is worth billions of dollars per annum (Kevan and Phillips, 2001; Kremen *et al.*, 2002) with both direct and indirect influences on the global economy (Gallai *et al.*, 2009; Status of Pollinators, 2006). Eighty percent of the world's agricultural crops are pollinated by *Apis mellifera* (Carreck and Williams, 1998); however, wild pollinators are

more important (Breeze *et al.*, 2011). Along with its crucial economic role, pollination also has an important ecological role. Pollination by bees helps maintain wild flower diversity in both managed and agricultural ecosystems. Furthermore, non-crop flowers can increase crop yield by providing additional resources for crucial pollinator species (Sheffield *et al.*, 2008). More generally, pollination helps to sustain all the other organisms in an ecosystem that depend on resources ultimately obtained from flowering plants.

Bees are the most important animal pollinators (Aizen and Feinsinger, 2003; Kremen *et al.*, 2007). There are over 19,700 known species of bees globally (Packer, 2010). Bees are present on every continent except Antarctica (Kearns *et al.*, 1998). Biodiversity surveys have indicated declines in bee populations (Allen-Wardell *et al.*, 1998; Biesmeijer *et al.*, 2006; Williams *et al.*, 2010). Despite the ecological and economic significance of bees, little is known about the response of wild bee communities to anthropogenic activities. This may be partly because different species respond differently to the same ecological disturbance (Winfree *et al.*, 2006).

Popular methods for quantifying bee biodiversity have included diversity indices (Shannon and Simpson indices), and community similarity indices. These methods are useful for showing changes in diversity over time. However, they are not particularly useful in identifying how the total number of bee species change through time. Perhaps, a better approach to examining community change is to use functional guilds rather than community structure as a whole (Grixti and Packer, 2006; Tilman and Lehman, 2001). A functional guild is a grouping of organisms with similar ecological, behavioral or life

history traits. Guilds are used to help us understand how different components of a community respond to perturbations or function together (Magurran, 2004).

Quantifying whether bee communities are healthy or suffering from the effects of disturbance is one of the most important endeavors in ensuring that pollination services are sustained. Species communities that fit lognormal distributions have order, function, and stability in species diversity (Grøtan *et al.*, 2012; Hill and Hamer, 1998; Hubbell, 2001; Magurran, 2004). Kevan *et al.* (1997) demonstrated that if a bee community does not fit a lognormal distribution then the community is said to be suffering from environmental interference.

One of the main questions of this thesis is whether examining bee community response by breaking the community into functional guilds (solitary ground nesters, social ground nesters, cavity nesters, bumble bees and cleptoparasites) provides more accuracy than examining bee communities as a whole (Neame *et al.*, 2012; Tilman and Lehman, 2001, Williams *et al.*, 2010).

1.2 Restoration Ecology and the Importance of Oak Savannah

The first restoration project began in 1935 under the supervision of Aldo Leopold and involved transforming farmland back to tallgrass prairie (Jordan *et al.*, 1987).

Farmland had been purchased by the University of Wisconsin in the town of Madison with the intentions of using the land for the University's Arboretum. During a speech at the dedication ceremony of the Arboretum, Leopold indicated that the land would be restored to a tallgrass prairie instead of constructing an arboretum. Within a decade of Aldo Leopold's actions, many began to voice their concerns that degraded landscapes needed urgent attention (Daigle and Havinga, 2000). As a result of many individuals speaking out regarding the state of ecosystems, in 1988 the Society of Ecological Restoration was formed. The society represents a broad array of individuals that are interested in promoting ecological restoration as a means of sustaining biodiversity (SER, 2004).

The Society of Ecological Restoration defines restoration ecology as "the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed" (SER, 2004). In the literature the terms restoration ecology and ecological restoration are often used interchangeably (Carins and Heckman, 1996). It is important to clarify that restoration ecology is simply the study of the ecological restoration of ecosystems (Clewell and Aronson, 2007).

In Southern Ontario, there have been many recovery campaigns employed in the past several decades, as landscapes have been degraded from years of urbanization and

industrial and agricultural development (Kurczeuski, 2000). Restoration projects implemented in Ontario have ranged from re-planting native seeds in newly restored urban gardens (Irvine *et al.*, 1998) to assistance in the recovery of the Sudbury area's watersheds after years of damage from industrial contamination (Gunn and Mills, 1998; Niagru *et al.*, 1998) and restoring Lake Simcoe's watershed (Palmer *et al.*, 2011).

Oak savannah is natural habitat that contains both woodland and meadow flora and fauna. Oak savannah is comprised of a moderately open canopy with no more than 50% tree coverage, well-drained sandy soils, and a diverse floral distribution in the understory (Lee *et al.*, 1998). These habitat characteristics provide optimal nesting and foraging conditions for bees (Taylor and Catling, 2011). Oak savannah has been reduced to 0.05% of its historical range throughout North America due to excessive anthropogenic activities (Nuzzo, 1986). In the past few decades the importance of this habitat has become well established with an increased need to conserve the fragments left (COSEWIC, 2000; Kurczeuski, 2000). Two oak savannah remnants were chosen for this study based on their size, integrity and known fire history: Pinery Provincial Park (henceforth Pinery) (43° 16.691'N; 81°48.696'W), Turkey Point Provincial Park (henceforth Turkey Point) (42° 42.117'N; 80° 20.262'W).

Pinery is arguably the largest intact oak savannah remnant in North America, roughly 2 532 ha in size and is located on the shores of Lake Huron (McKenzie, personal communication). Since recognition in the early 1980's as prime oak savannah habitat, restoration efforts in the form of prescribed burn plans, deer exclosures, and removal of invasive species have taken place (Bakowsky, 1995).

Turkey Point was established in 1959 and is located on the north shore of Lake Erie. A prescribed burn plan was introduced based on recommendations following a vegetation survey in 1992 (Lee *et al.*, 1998). The survey (Lee *et al.*, 1998) showed over abundance of fire-intolerant species such as bracken fern (*Pteridium aquilinum* Kuhn) and poison ivy (*Rhus radicans* Kuntze) since the use of fire as a tool for maintaining diversity ceased in the 1980's. The cessation of fire also led to an increased canopy cover and increased abundance of ground litter.

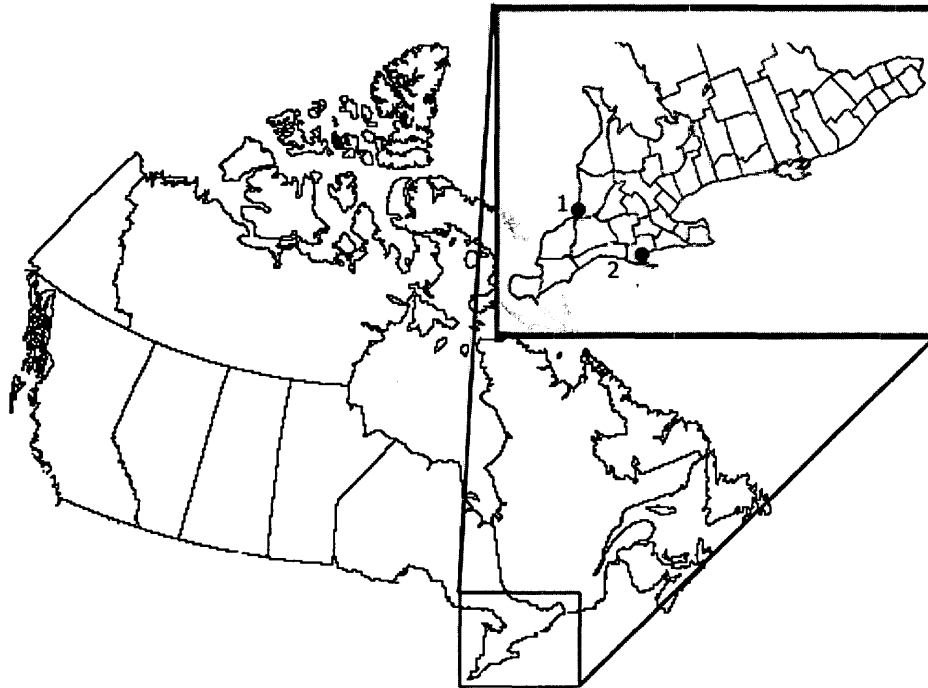


Figure 1- Map showing field localities (1) Pinery Provincial Park, and (2) Turkey Point Provincial Park in Southern Ontario, Canada.

1.3 The importance of fire in ecosystems

The pattern of fires in natural ecosystems has changed dramatically in the last few centuries. Although lightning strikes are said to have caused many fires throughout history, in recent decades 90% of fires have been human induced whether intentionally or through negligence (Myers, 2006). The history of fire in the ecological landscape is closely associated with the patterns of movement of human beings (Pyne, 1984).

In Southern Ontario, for instance, aboriginal communities used fire as a technique to maintain land for campsites, agricultural purposes, and grazing for animals (Bakowsky and Riley, 1994). Aboriginal communities used fire as a tool for clearing land for agricultural purposes but not to the same extent as did the early European settlers (Bakowsky and Riley, 1994; Pyne, 1984). Shortly after the arrival of Europeans to North America land was cleared for large-scale agricultural production. European communities were more sedentary than Aboriginal ones, and this ultimately led to the suppression of fire (Pyne, 1984). To some degree, fire suppression still occurs today (Backer *et al.*, 2006).

In Southern Ontario fire is used as a tool for restoring oak savannah habitat through controlled burning (Lee *et al.*, 1998). Prescribed burns are intentional fires that are set under specific conditions (Peterson and Reich, 2001). The end goal of performing controlled burns is to maintain ecological integrity of habitats. Ecological integrity is the abundance and diversity of organisms and the ecological patterns and processes responsible for biological diversity (van Kooten *et al.*, 2000). Such characteristics

include composition and abundance of native species and the presence of natural disturbances. Fire is an important factor in maintaining ecological integrity and biodiversity, especially in tallgrass and oak savannah remnants (Lavorel *et al.*, 2007).

Fire regime is defined as re-occurring conditions that characterize an ecosystem (Myers, 2006). Fire regimes encompass the severity, frequency, seasonality, and spatial components of fire. A balanced fire regime is key to maintaining ecological integrity of fire-dependent habitats. For instance, knowing that fuel directly influences intensity; controlled fires in northeastern regions of North America occur in the spring season rather than summer or fall and are classified as low intensity surface fires (Tester, 1996). This is because plant species will be damp from winter conditions and will be less of a fuel source than would be present in the summer months. If fires did occur in summer months rather than the spring, the habitat conditions could be altered drastically such that the integrity of the ecosystem is jeopardized (Sugihara *et al.*, 2006). Furthermore, fires conducted in the spring months promote native vegetation, whereas late summer early fall burns support the establishment of invasive species (Tester, 1996).

Fire ecology is defined as a field of study that examines the effect of fire on ecological functions (Pyne, 1984). Forty six percent of all terrestrial ecosystems worldwide are fire-dependent (Myers, 2006). Fire dependent ecosystems are habitats where fire is required for the overall function and stability of the ecosystem (Wright and Bailey, 1982). In the past, many have argued that fire should be seen as a disturbance that hinders the overall function and balance of an ecosystem (Collins and Glenn, 1997; Pickett and White; 1985) and ecosystems that are disturbed will return to stable states on

their own without the presence of fire (Mohr, 1992; Parr and Brockett, 1999). Fire ecology is reemerging at the forefront of conservation and land management as damaging, unusually large and/or intense wildfires worldwide have societies re-thinking the importance of fire in ecosystems.

The fauna of an ecosystem, unlike its flora, does not contribute to fire in the form of fuel; but only reacts to the effects of fire (Sugihara *et al.*, 2006). Unlike plants, most faunal species are mobile enough to escape fire and move to unburned patches of habitat. Effects of fire on faunal composition of a habitat are directly related to how modified the habitat is from the fire and this in turn depends upon the detailed attributes of a specific fire (Sugihara *et al.*, 2006). Far more literature exists on the impacts of fire on flora than on the fauna in ecosystems (Clarke, 2008). This is mostly because animals have the ability to retreat when fire occurs. This makes measuring how animals respond to fire far more challenging but it remains important nonetheless.

To ensure that the integrity of ecosystems is not lost, land managers must execute controlled burns so species are not made vulnerable due to attributes associated with wild fires (i.e. severity, frequency, size) (Myers, 2006). Habitats receiving fire treatment should be next to unburned habitat patches that contain similar ecological communities. Fauna will utilize unburned habitat patches close in proximity as habitat refugia (Sugihara *et al.*, 2006).

The habitat refugium hypothesis is based on the notion that a healthy ecosystem is comprised of habitat mosaics. Habitat mosaics can support different community assemblages over space at the same time (Parr and Brockett, 1999; Sugihara *et al.*, 2006).

Fire can be used as a tool to create habitat mosaics and in turn maintain biodiversity and ecological integrity. This is known as the patch mosaic-burning concept (Parr and Anderson 2005), which suggests that if fire attributes vary over space and time biodiversity of a habitat will increase (Parr and Brockett, 1999). That is, pyrodiversity enhances biodiversity (Bradstock *et al.*, 2005; Parr and Anderson, 2006).

Determining how ecosystem constituents respond to fire is not easy but is important in deciding how fire is to be used in habitat management. It is clear that the physical attributes of fire can seriously alter or enhance biodiversity of an ecosystem. Fire has been and will continue to be an integral part of ecosystems and this thesis aims to increase our understanding of its impact upon bee communities.

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Chapter 2- Fire disturbance and bees: a test of the intermediate disturbance hypothesis.

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2.1 Abstract

Understanding how disturbances such as fire affect bee species diversity could be crucial to conserving pollination services in disturbance dependent habitats. Disturbances increase bee species diversity, however, no study has ever tested the intermediate disturbance hypothesis (IDH) as it applies to bees. Here we tested for the first time, the IDH for bee species in oak savannah habitat in Southern Ontario, Canada. Species richness, α diversity and evenness were quantified in 3 burn categories: fresh burn, intermediate burn and mature burn, along with control sites over four years (from 2007 to 2010). We found support for the IDH in maximizing bee species diversity. Bee diversity was higher in years directly following fire disturbance than compared to many years post fire. Differences across burn categories were stronger for species richness than species diversity and evenness. Species diversity varied across burn categories and evenness was higher many years post fire than compared to recently burned sites. Understanding the importance of environmental disturbances such as fire in maintaining bee species diversity in ecosystems is crucial, if the pollination services bees provide are to be sustained. Results show that bee diversity is enhanced at an intermediate time in fire dependent habitats. Due to the experimental nature of our study, we were able to demonstrate that bee diversity is greater shortly after fire disturbance than many years after.

2.2 Introduction

The Intermediate Disturbance Hypothesis (IDH) (Connell, 1978) states that maximum species diversity is reached in habitats with moderate disturbance (Connell, 1978; Wilson, 1990). That is, species diversity is enhanced by spatial and temporal heterogeneity of disturbances that keep communities from reaching a state of equilibrium (D'Odorico *et al.*, 2008). Support for the IDH has come from studies of numerous habitats and taxa ranging from benthic stream species (Frouin, 2000) to tropical forest trees (Molino & Sabatier, 2001). Previous studies that have demonstrated the importance of the intermediate disturbance hypothesis in maintaining species diversity in habitats have examined the role experimentally (Biswas *et al.*, 2010; Beckage and Stout, 2000; Huxham *et al.*, 2000).

Some ecosystems require naturally occurring disturbances in order for them to attain peak levels of biodiversity in both flora and fauna (Myers, 2006). Oak savannah in Southern Ontario is such a habitat as it is fire prone and requires occasional fire to maintain high species diversity (Daigle & Havinga, 2001; McEwan *et al.* 2011). Presently, this habitat type occupies a tiny proportion of its previous range, which was from the Ottawa valley south to Windsor (Kurczeuski, 2000). Significant progress has been made in understanding the restoration needs of this habitat (Brudvig, 2010). One restoration method has been the re-introduction of fire (Harrington & Kathol, 2009), performed through prescribed burns, which are set under pre-determined conditions (Peterson & Reich, 2001). Considerable post restoration monitoring is needed to understand how a habitat responds to a restoration practice (Matthews & Spyreas, 2010).

Thus it is essential to understand community composition before trying to understand how a habitat responds to any particular restoration practice. In oak savannah, quantifying species diversity within the first 5 years post fire is particularly critical because it is an intermediate successional stage that is attained within 12 years after a burn (Lee *et al.* 1998).

As habitats become increasingly disturbed, ways of rapidly determining which habitats to conserve are becoming essential (Ricketts *et al.*, 2001; Steffan-Dewenter, 2001; Hess *et al.*, 2006). One approach to this problem is the use of indicator taxa as a proxy for overall biodiversity (Kerr *et al.*, 2000). Indicator taxa are measurable surrogates for environmental attributes that are of importance to society (Noss, 1990). In theory, the diversity of the indicator taxa should reflect the diversity and state of other taxa within a given ecosystem and also be sensitive to small population size (Ricketts *et al.*, 1999; Kerr *et al.*, 2000). Choosing a taxon that is not present in diverse ecosystems decreases its reliability to indicate the state of other ecosystems (Soberón *et al.*, 2000; Zayed & Packer, 2005; Packer, 2010). Selecting taxa to be bioindicators is not an easy task. A preferred method for selecting ecological indicators is using a hierarchical approach (Noss, 1990) reporting on the status of an ecosystem at many levels of biological organization rather than just one (Soberón *et al.*, 2000). The assumption is that different levels of biological organization respond differently to different environmental pressures. Thus, by only reporting from a single organizational level, the true complexity of the habitat has not been represented (Noss, 1990; Kremen, 1992).

Pollination services and pollinators are crucial ecological importance in most of the world's terrestrial ecosystems (Potts *et al.*, 2010). With almost 20 000 species known worldwide (Packer, 2010), bees are by far the most important animal pollinator (Breeze *et al.*, 2011). Consequently, understanding how bee species respond to environmental disturbance is important to ensure pollination services are sustained. Studies have demonstrated not only the decline of bee communities (Allen-Wardell *et al.*, 1998; Kearns *et al.*, 1998; Biesmeijer *et al.*, 2006; National Research Council, 2006), but also the vulnerability of different bee guilds to disturbances such as, grazing, tilling, and fire (Winfree *et al.*, 2009; Williams *et al.*, 2010).

Works that have examined the effects of fire disturbances on bees have suggested that bee communities were at their highest diversity levels post-disturbance (Potts *et al.*, 2001; Moretti *et al.*, 2009). That is, fire increases bee biodiversity. It is known that bee diversity is at its peak soon following fire disturbance (< 5 years), but high diversity is almost always short-lived (Potts *et al.*, 2003). By an intermediate time (10-15 yrs.) post fire, bee diversity was significantly less than previously (Potts *et al.*, 2001). However, although these studies quantified bee diversity within 5 years of fire disturbance, they were not able to report on the pre-disturbance bee community. This was in most part due to the historical nature of the studied disturbance. The lack of pre-disturbance species sampling in disturbance-response studies is problematic, as is the lack of experimental verification (Moller *et al.*, 2004).

The primary objective of this study is to test experimentally the hypothesis that bee diversity is greater shortly after fire disturbance than many years after. To our

knowledge, no study has explicitly tested this hypothesis experimentally. This study not only reports on the pre-disturbance bee community but, because of the unique sampling design, we are able to investigate changes in bee diversity in response to fire disturbance over time. In this study, fire will act as an intermediate level of disturbance in the temporal sense, because we sampled the same oak savannah habitat over 4 years where fires had been set at the beginning of year one in some sites, and at ages of 10-15 previously at others. Furthermore, for the recent fires, we had pre-fire baseline data for comparison as well as control sites that had not been burned (or burned naturally) within living memory. We predict that bee species diversity will peak at an intermediate time after a fire and that bee diversity decreases thereafter.

2.3 Methods

2.3.1 Study Sites and Fire History

Pinery Provincial Park ($43^{\circ} 16.691'N$; $81^{\circ}48.696'W$)(henceforth Pinery) is arguably the largest intact oak savannah remnant in North America (McKenzie, pers com). Pinery is roughly 2 532 ha and is located on the shores of Lake Huron (Figure 1). It opened to the public for recreational purposes in 1959. The southeast shore of Lake Huron, cottages, recreational properties and agricultural land surround the park.

The park was logged during the 1960's and a pine plantation was established. Over 3 500 000 pines were planted to close in the canopy from the logging practices

which historically took place throughout the park (Carins, personal communication).

Since recognition in the early 1980's as prime oak savannah habitat, restoration efforts in the form of prescribed burn plans, deer exclosures, and removal of invasive species have taken place (Bakowsky, 1995; Bazely *et al.*, 1997). Currently the park consists of many recreational areas, roads, campsites, and patches of oak savannah of various qualities.

Turkey Point Provincial Park (42° 42.117'N; 80° 20.262'W)(henceforth Turkey Point) was established in 1959 and is located on the north shore of Lake Erie and is surrounded by agricultural, and recreational land including a golf course to the south as well as the lake. A prescribed burn plan was introduced based on recommendations following a vegetation survey in 1992. The survey showed over abundance of fire-tolerant species such as *Pteridium aquilinum* Kuhn (Bracken fern) and *Rhus radicans* Kuntze (Poison Ivy). The park includes various campsites, and recreational areas that are highly disturbed with little understory growth as well as compacted soils.

In this study, a locality is defined as a provincial park, whereas site is defined as a burn area within a locality and a pan trap plot is defined as 30 pans separated 3m from each other within a site. Each locality consisted of various burn types: fresh burns (< 2 years), intermediate age burns (5-10 yrs), mature burns (15-25 yrs) and control sites that have not been burned (Table 1). The control site at Pinery was approximately 25 ha in size, while the control site at Turkey Point was 5 ha. Freshly burned sites at both localities were burned in the spring of 2008. The fresh burn at Pinery was 60ha: the largest controlled low intensity fire to occur in the parks history. Prior to being burned in 2008, there was no known burn history for the last 50-100 years for either locality.

Intermediate burn sites at Pinery were burned in 2000 whereas intermediate burn sites at Turkey Point were burned in 2003. The intermediate burn site at Pinery was located south of the fresh burn site and southeast of Lake Huron and was 50 ha in size (Figure 1 and 2). The intermediate burn site at Turkey Point was located east of the fresh burn site and was approximately 18 ha in size (Figure 2). Both mature burn sites were burned in 1993 and were approximately 50 ha and 15 ha in size respectively for Pinery and Turkey Point. The mature burn site in Pinery was located in the southernmost corner of the park; whereas in Turkey Point it was located at the northern park boundary (Figure 2). Each sampling site was approximately 0.3 km from the edge of a burn type to minimize edge effects.

Knowing that the amount of fuel directly influences fire intensity; most controlled burns in northeastern regions of North America occur in the spring season rather than summer or fall (Suigihara *et al.*, 2006). This is because damp conditions make available fuel burn less readily and the resulting fires easier to control in the summer months (Tester, 1996). Summer fires would have a more drastic impact because they would burn at a higher temperature such that the integrity of the ecosystem would be jeopardized (Sugihara *et al.*, 2006). Furthermore, fires conducted in spring in Oak Savannah promote native vegetation, whereas late summer/early fall burns support the establishment of invasive species (Tester, 1996). All fires conducted in each provincial park occurred in spring and were classified as low intensity surface fires that only burn through dead plant material on the ground and do not kill trees or result in combustion of the organic materials in the soil below.

2.3.2 Bee Sampling and Identification

For this study pan traps were the chosen method of sampling because of their low-cost, simplicity, and their ability to effectively sample relative abundance and species richness of bees (Kirk 1984; Leong & Thorp, 1999; Bartholomew & Prowell, 2005; Campbell & Hanula, 2007). Pan traps are also better at sampling parasitic species that are rarely found on floral resources (Roulston *et al.*, 2007). This feature of pans is extremely desirable for this study as recent studies on fire and bees have shown that parasitic species are one of the first groups to respond after the presence of fire within a habitat (Moretti *et al.*, 2009).

Pan trap plots were in an X formation with bowls 3m apart with alternating pan colours- yellow, blue and white, following the sampling protocol put forth by Droege *et al.*, (2003) (Figure 1). Transects of 1km length had a total of 3-5 arrays, to give replication within each transect. Pan traps were set from 8:00h-17:00h each collecting day. Collecting took place every 10 days from May until September 2007-2010 to ensure that all species' flight periods are sampled giving a total of 12 campaigns per year.

All specimens were identified to species level using various keys (Mitchell 1960a & 1960b; Packer *et al.*, 2007; Polistes Corporation, 2007). Other keys used for specific taxa were, Gibbs (2010) for metallic *Lasioglossum* spp.; McGinley (1986) for *Lasioglossum sensu strictu*; Romankova (2003) for *Colletes* spp. and Lavery and Harder (1988) for *Bombus* spp. *Megachile* spp. and *Osmia* spp. were verified by Dr. Cory

Sheffield, *Bombus* spp were verified by Sheila. R. Colla. All specimens are housed at the York University Bee Collection (PCYU), Toronto, Ontario, Canada.

2.3.3. Statistical Analysis

Samples from each park were analyzed across burn treatments from 2007 to 2010 in order to quantify the temporal effect fire has on bee species diversity compared to the control treatment. Changes in bee diversity were examined using biodiversity estimates: species richness (S), diversity (H') and evenness (J) with Species Richness and Diversity 4 software (Pisces Conservation Ltd.) (Seaby & Henderson, 2006). S is the total species richness, H' is Shannon's index of diversity, $H' = -\sum p_i \ln(p_i)$ (where p_i is the proportion of the sample belonging to species i and evenness was defined as $J = H'/\ln(S)$) (Magurran, 2004; Krebs, 1999). Diversity and evenness results were adjusted for multiple comparisons using the Bonferroni correction method (Milton, 1999). These measures were chosen as they are the fundamental ways of indicating changes in diversity (Krebs, 1999) and have been routinely used to quantify changes in disturbed habitats (e.g. Biswas *et al.*, 2010; Pfaf *et al.*, 2010), including studies of bees (Grixti & Packer, 2006). A pairwise t-test was used to statistically test differences in biodiversity metrics between control sites and burns sites in each locality. All raw data from this study are available at www.yorku.ca/bugsrus/index.

2.4 Results

A total of 11323 bees were collected from May 2007 to October 2010. Twenty-one genera and 183 species were found at Pinery, 22 genera and 159 species were found at Turkey Point (Appendix A).

The control sites (Site1) in both Pinery and Turkey Point showed variation in the total number of species captured over time (Figure 2). Both the Shannon index of diversity and the evenness measure showed variation across sampling years with a trend that was generally decreasing (Figure 3).

Neither the intermediate nor mature burn sites at each locality differed significantly over time compared to the control site (Table 2 and 3) (Figure 2 and 3). Species diversity peaked in both habitats in 2008 and by 2010 species diversity was at its lowest but with high species evenness (Figure 3 and 4). Species richness in the intermediate burn sites (Site2) at both localities showed a decline from 2007 to 2010 (Figure 2). The intermediate burn compared to the control site exhibited a significant decrease in 2007 at Pinery in both diversity and evenness (Figure 3 and 4). Evenness values in 2009 at Pinery among the control and intermediate burn did reveal a significant decrease (Figure 4).

In contrast to the overall decline in biodiversity estimates of the older burn sites, the fresh burn sites showed considerable temporal variation in biodiversity estimates compared to the control. The freshly burned sites had the lowest species diversity during the year of the fire (2008) (Figure 3) but species richness and diversity soon rebounded to

pre fire year (2007) levels. When the control was compared to the freshly burned site at Pinery across sampling years, the only significant difference in species diversity among sites was in 2008 (Table 2). There were no significant differences in evenness values across all collecting years between the freshly burned site and the control (Table 2). Species richness in Turkey Point showed a similar trend to results from Pinery: a dramatic decrease from pre fire to the fire disturbance year (Figure 2). The freshly burned site (Site4) at Turkey Point showed a significant difference in diversity when compared to the control site in 2007 (Table 2). Even though other multiple comparisons did not reveal significant difference among the control and freshly burned site, Turkey Point did exhibit the same trend as seen in Pinery, whereas biodiversity parameters were highest following fire.

2.5 Discussion

This study is the first experimental test of the IDH applied to bee communities. We found support for the IDH: bee diversity increased at an intermediate time period following an experimental, low intensity burn. Support for the IDH was more evident in changes in bee species richness over time in both localities, compared to other biodiversity estimates: species diversity and evenness (Figure 2).

We found that biodiversity in the control sites at both parks decreased in overall diversity from 2007 to 2010 but increased in evenness (Figures 3 and 4). The variation in

species richness and decline in biodiversity parameters across years in Pinery and Turkey Point could be due to the lack of fire at each site, as neither site has been burned in the last 100 years. Because oak savannah is a fire dependent habitat (Daigle & Havinga, 2001) and neither control site was indicative of early successional habitat (Figure 6) our results show that the bee species community at control sites may not be one that is representative of oak savannah habitat. An early successional habitat is comprised of fast growing shrubs with few mature trees and mostly grasses and wildflowers in the understory (Asking, 2001). Both control sites contained an over abundance of mature trees, overgrown shrubs with very few wildflowers present (Figure 4). Increased evenness and decreased species diversity show that habitat conditions were not suitable for a diverse oak savannah bee community and perhaps only more advanced successional stage tolerant species were able to withstand the overgrown habitat conditions

Though vegetation was not measured in this study, previous work has shown that freshly burned habitat is comprised of higher floral diversity compared to post fire habitat (i.e. 15-20 years after a fire) (Bengtsson *et al.* 2000). Patterns of bee species diversity observed immediately post fire disturbance agrees with literature that has linked patterns of bee species diversity to changes in floral diversity post disturbance (Moretti *et al.*, 2009; Potts *et al.*, 2003).

The intermediate burn site in both localities showed higher values for species richness and other biodiversity estimates during the first two collecting years (2007 and 2008) compared to the last two (2009 and 2010) (Table 2 and 3). This result is direct support for the importance of the IDH in maintaining bee diversity after an intermediate

amount of time, species diversity decreased. In both localities, the last disturbance occurred 10 years before the initial collecting year (2007). An intermediate successional habitat such as oak savannah reaches maturity by 12 years (Lee *et al.*, 1998). Therefore, by the final collecting year (2010), the habitat was closer to 15 years since disturbance and becoming reminiscent of a mature oak forest rather than an intermediate successional stage oak savannah.

The mature burn site at Pinery showed a significant decline in species richness from 2007 to 2010. This is more evidence that bee diversity continues to decline many years post disturbance compared to 1-3 years after fire disturbance. This result is echoed in Turkey Point as over time species richness, diversity and evenness all declined (Table 2). One of the crucial components of this study was the pre-disturbance sampling. Because of the experimental nature of the work, our conclusions on the importance of the IDH in maximizing bee diversity are more concrete than if the results had been based solely on a historical disturbance event as has hitherto been the case (Potts *et al.*, 2001; Potts *et al.*, 2003; Winfree *et al.*, 2009). Perhaps one of the most interesting results from this study was how quickly bee species richness responded to the fire treatment in freshly burned habitats. It was expected that post-disturbance bee diversity would be lower than pre-disturbance diversity, however, it was not anticipated that biodiversity estimates within two years of fire would be similar to the pre-disturbance year (Table 1). High species evenness and low diversity in both parks indicate that initial post-disturbance habitat conditions were likely only suitable for a small number of bee species but many individuals of those species were collected. A plausible explanation is that fire

disturbance in oak savannah immediately eliminates leaf litter, and ground debris (Daigle & Havinga, 2001), providing more potential nest sites for ground nesting bees over species that prefer substrates like cavities (i.e. twig nesters) (see chapter 3 for an assessment of bee guild responses to experimental fires).

Even though fire disturbance can create deadfall from burned vegetation, which is good substrate for cavity nesters (Cane *et al.*, 2007), such habitat components are less common in very early succession stages. Over time, as a habitat matures from early succession stages, the increase in nesting substrates and floral resources, improve the suitability of the habitat for bee species. Bee species diversity improves; evenness of species is lower and the community shifts from moving towards equilibrium and becomes more heterogeneous.

Overall, changes in bee diversity at Pinery were more obvious than the results from Turkey Point (Figure 3). This could be due to the fact that each treatment habitat sampled at Pinery, is much larger than the treatment habitat sampled at Turkey Point. Bee species found at Pinery could be responding *in situ* to fire disturbance whereas bees sampled at Turkey Point might have been moving into the sampled area from outside. That is, bee species could use unburned habitat patches as refugia in close proximity to burned patches in Turkey Point and be less affected by disturbance compared to Pinery. The greater the spatial scale of the area burned the further fauna species will have to disperse and the longer it will take to recolonize resulting in lower diversity levels (Sugihara *et al.*, 2006). Even though, species movement throughout treatment areas is

easier because of spatial proximity at Turkey Point, both localities did show that bee diversity is highest shortly after fire than many years post fire.

In conclusion, this study was successful in verifying the IDH and the role of intermediate levels of disturbance in maintaining bee diversity. The experimental nature of this study provided strong support for the hypothesis compared to published studies that indicated bee diversity increases with disturbance based on historical data only. Results showed that bee diversity is maximized by moderate disturbance such as fire in habitats shortly after disturbance compared to many years post disturbance. We also showed that bee diversity can rebound rapidly (within 2 years) from fire disturbance in savannah habitat.

2.7 References

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2.8 Figures and Tables

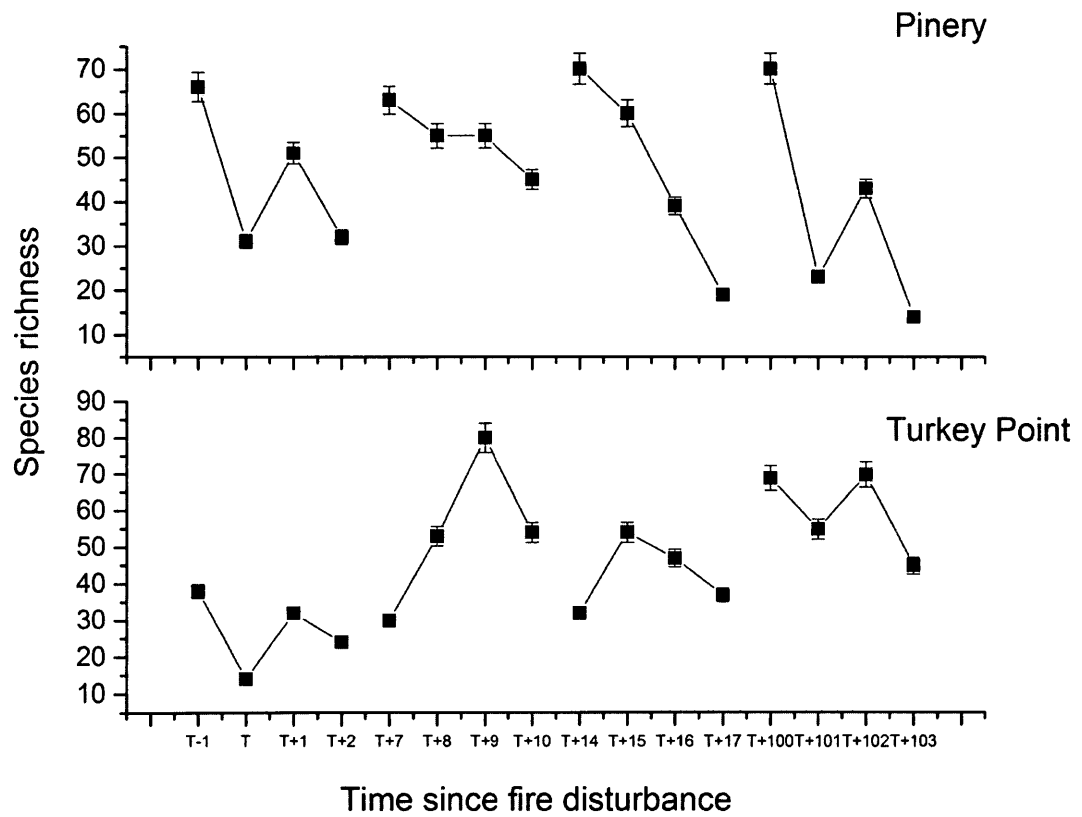


Figure 2- Species richness values and standard error at fresh, intermediate and mature, and control site at Pinery and Turkey Point.

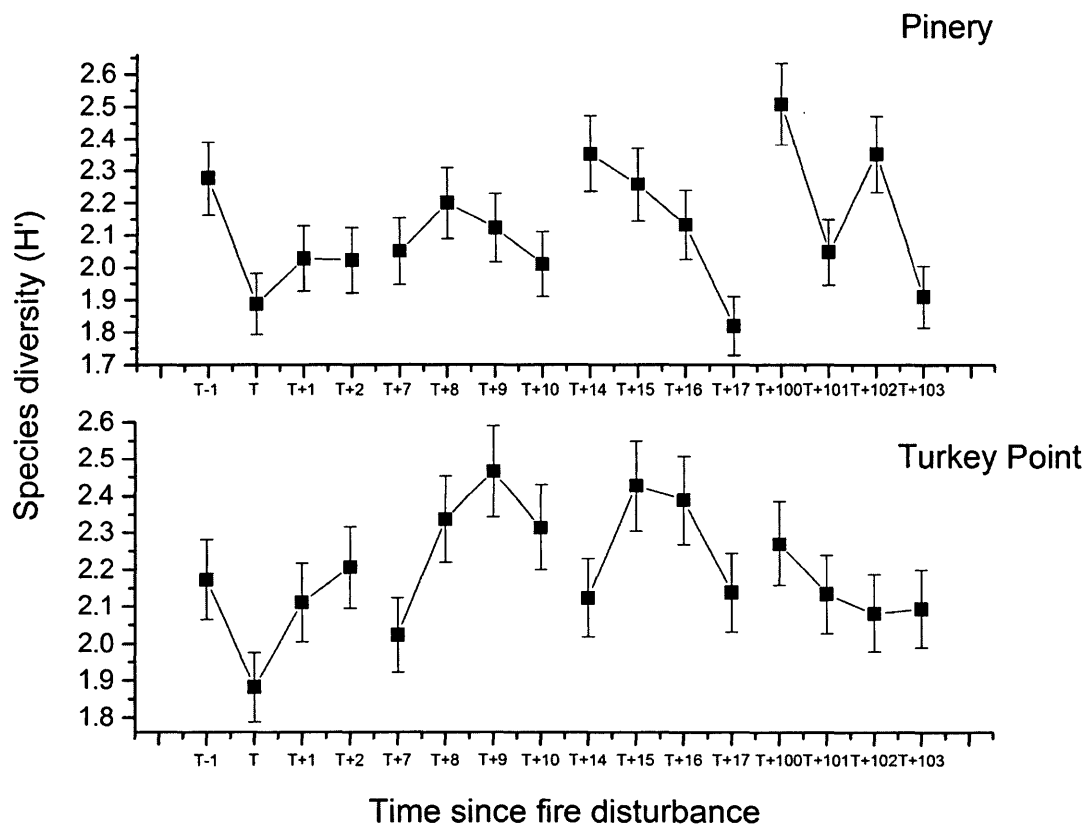


Figure 3- Species diversity (H') values and standard error at fresh, intermediate and mature, and control site at Pinery and Turkey Point.

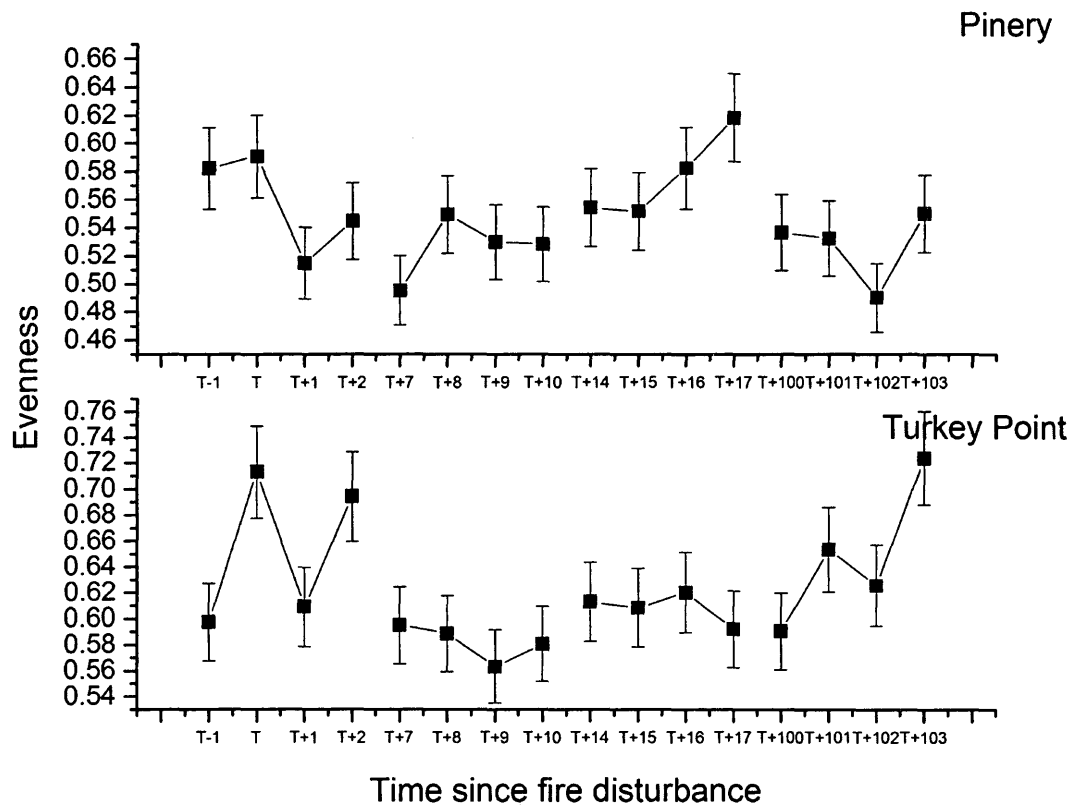


Figure 4- Evenness (J) values and standard error at fresh, intermediate and mature, and control site at Pinery and Turkey Point.

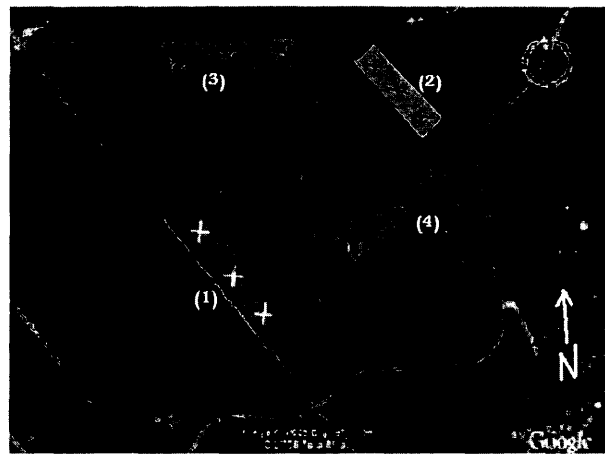
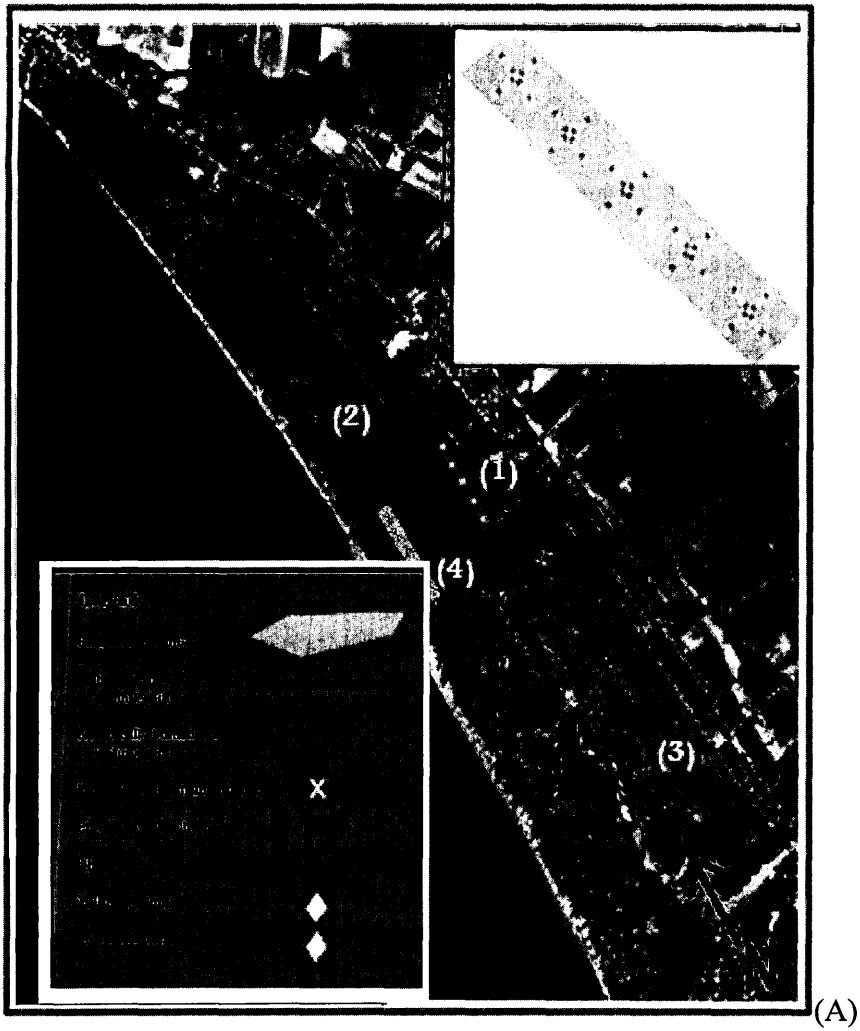


Figure 5- Schematic diagram of sampling design in each locality: (A) Pinery Provincial Park, (B) Turkey Point Provincial Park, and (C) legend indicating burned and unburned sites and pan trap plots per burn site: (1) control site, (2) fresh burn, (3) mature burn, and (4) intermediate burn.

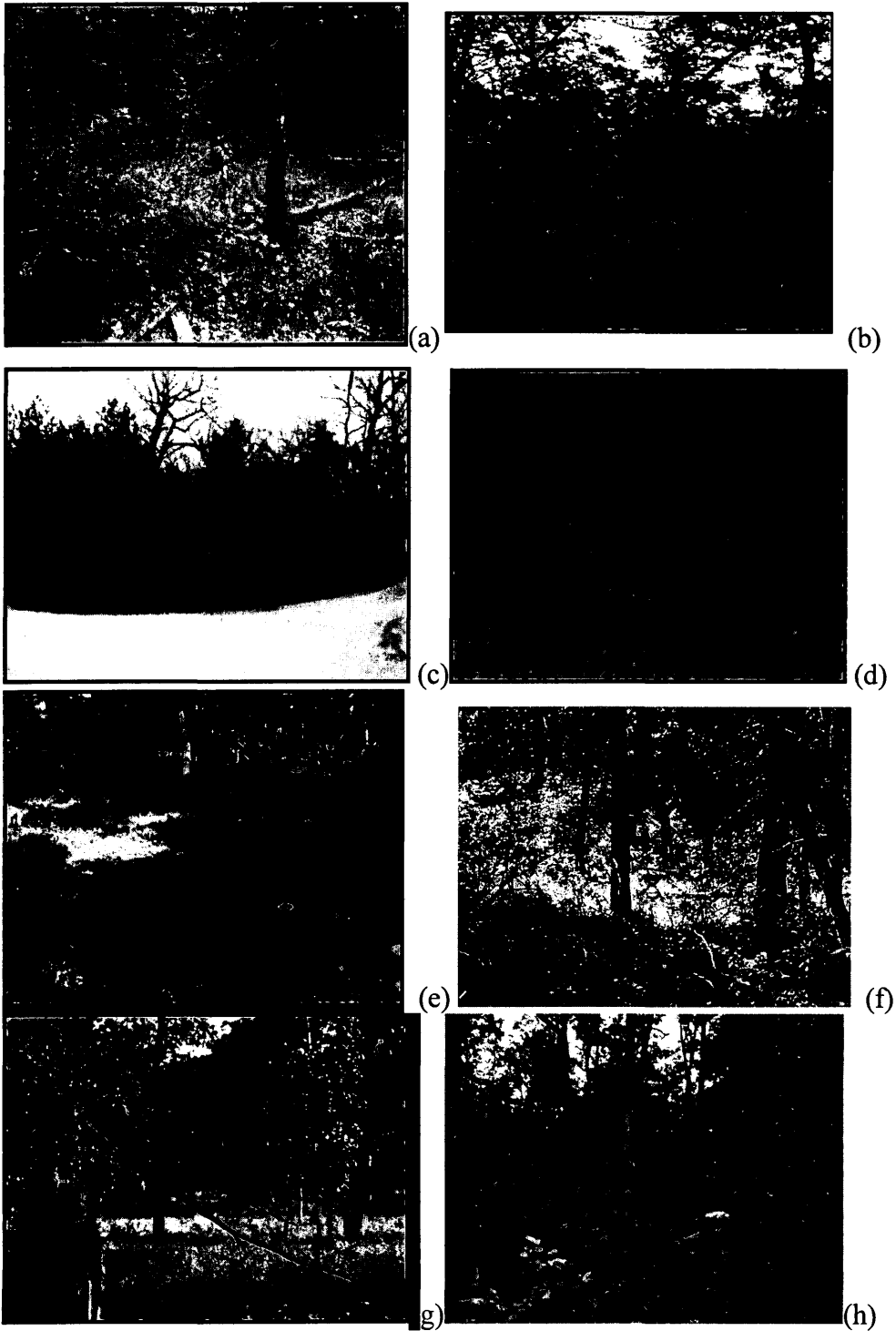


Figure 6- Images of each burn site at Pinery Provincial Park: (a) control, (c) fresh burn, (e) intermediate burn, (g), mature burn and Turkey Point Provincial Park: (b) control, (d) fresh burn, (f) intermediate burn, and (h) mature burn. Note the pan trap array in figure 3e.

Table 1- Number of sites from each locality, Pinery and Turkey Point, grouped by various burn treatments with burn year associated with treatment and locality.

Fire frequency	Locality				Site Total
	Pinery	Burn Year	Turkey Point	Burn Year	
Control (unburnt)	5	N/A	3	N/A	8
Fresh fire (0-2 yrs)	5	2008	3	2008	8
Intermediate fire (5-10 yrs)	5	2000	3	2003	8
Mature fire (15-20yrs)	5	1993	3	1993	8
Totals	20		12		32

Table 2- Comparisons of Shannon-Wiener and Evenness values between experimental (sites 2-4) and control areas (site 1) for Pinery samples. Bolded comparisons indicate significant difference $p < 0.05$.

Comparison	<i>H'</i> Difference	P	E Difference	P
Site1 2007 vs. Site4 2007	0.0062	0.073	0.0458	0.07
Site1 2008 vs. Site4 2008	0.2460	0.004	0.0582	0.57
Site1 2009 vs. Site4 2009	0.0544	0.70	0.0138	0.50
Site1 2010 vs. Site4 2010	0.0711	0.32	0.0056	0.84
Site1 2007 vs. Site2 2007	0.2196	0.002	0.0413	0.009
Site1 2008 vs. Site2 2008	0.0673	0.35	0.0168	0.42
Site1 2009 vs. Site2 2009	0.0512	0.76	0.0397	0.05
Site1 2010 vs. Site2 2010	0.0831	0.31	0.0219	0.29
Site1 2007 vs. Site3 2007	0.0830	0.30	0.0177	0.33
Site1 2008 vs. Site3 2008	0.1249	0.13	0.0191	0.60
Site1 2009 vs. Site3 2009	0.0513	0.76	0.0922	0.30
Site1 2010 vs. Site3 2010	0.2754	0.15	0.0680	0.63

Table 3- Multiple comparisons among Shannon-Wiener and Evenness values for Turkey Point samples. Bolded comparisons indicate significant difference between H' values and E values at p<0.05.

Comparison	H' Difference	P	E Difference	P
Site1 2007 vs. Site4 2007	0.3345	0.04	0.0072	0.82
Site1 2008 vs. Site4 2008	0.1665	0.61	0.0598	0.52
Site1 2009 vs. Site4 2009	0.2418	0.18	0.0164	0.68
Site1 2010 vs. Site4 2010	0.2951	0.55	0.0300	0.83
Site1 2007 vs. Site2 2007	0.4844	0.0001	0.0046	0.85
Site1 2008 vs. Site2 2008	0.2880	0.22	0.0648	0.48
Site1 2009 vs. Site2 2009	0.1138	0.63	0.0627	0.61
Site1 2010 vs. Site2 2010	0.2951	0.60	0.1437	0.56
Site1 2007 vs. Site3 2007	0.3832	0.07	0.0228	0.79
Site1 2008 vs. Site3 2008	0.3785	0.10	0.0449	0.54
Site1 2009 vs. Site3 2009	0.0344	0.85	0.0055	0.90
Site1 2010 vs. Site3 2010	0.2264	0.75	0.1321	0.40

Chapter 3- Fire disturbance and functional diversity: bee guild responses to experimental fire treatments.

To be submitted for consideration for publication to the Journal of Insect Conservation and Diversity

3.1 Abstract

Understanding how environmental disturbances such as fire alter bee community composition is vital for maintaining bee community health in ecosystems. Studies have shown changes in bee community composition are more detectable at the functional guild level rather than examining changes in bee community biodiversity indices as a whole. The main objective of this study was to examine the effects of fire disturbance on functional guild diversity in habitats with different burn histories: freshly burned (<2yrs since fire), intermediate (5-10 yrs since fire), mature (15-20 yrs since fire) and control sites in two prime oak savannah habitat in Southern Ontario. Functional guilds examined were solitary and social ground nesters, cavity nesters, *Bombus* spp. and cleptoparasites. Different guilds responded differently to fire treatment, and the relative proportional abundance of species within guilds varied in burned habitat compared to the control and over time. The proportional abundance of solitary ground nesters increased post fire whereas the proportion of cavity nesters decreased. Cleptoparasites showed a significant increase in proportional abundance immediately post fire. *Bombus* spp. did not show significant changes in their relative proportional abundances over time among localities. Community composition analyses revealed similarities in guild composition among burned sites within localities and over time. No collecting years from Turkey Point fit a lognormal distribution whereas species distribution pre fire and from intermediate burned habitat at Pinery did fit a lognormal distribution.

3.2 Introduction

Conventional metrics for quantifying changes in biodiversity in ecosystems focus on parameters such as alpha and beta diversity (Krebs, 1999; Magurran, 2004). Though these metrics are understood to be fundamental, they are not adequate for evaluating how community composition is affected by environmental change (Larsen *et al.*, 2005, Tilman and Lehman, 2001).

Functional guilds are known to perform better in assessing community change (Gixti and Packer, 2006; Hoehn *et al.*, 2008; Tilman *et al.*, 1997; Sheffield *et al.*, 2013). Functional guilds are groups of species with similar ecological, behavioural or life history traits that can be used to understand how these biological attributes influence community response to environmental changes (Tilman and Lehman, 2001; Williams *et al.*, 2010). Until recently, functional guilds have been used mostly to assess plant communities (Lavorel and Garnier, 2002).

Bees are without question the single most important taxonomic group of pollinators (Aizen and Feinsinger, 2003; Kremen *et al.*, 2007). Determining whether or not bee communities are suffering from environmental degradation is vital to not only ensure maintenance of the pollination services they provide, but also to sustain other organisms that ultimately rely on floral resources (Winfree, 2010).

Previous studies on bee communities have demonstrated declines due to human disturbances and have shown that many factors such as fire, pesticide use, tilling and grazing affect patterns of bee diversity and abundance (Biesmeijer *et al.*, 2006; Winfree *et al.*, 2006; Williams *et al.*, 2010). Studies have either investigated how environmental

changes have affected functional diversity of bees (Moretti *et al.*, 2009) or have assessed bee community change over time (Grixti and Packer, 2006; Williams *et al.*, 2001).

Knowing that bee communities respond to disturbance within habitats (Neame *et al.*, 2012; Potts *et al.*, 2003; Williams *et al.*, 2010) and bee community change is better assessed at the guild level (Grixti and Packer, 2006), we examine the effects of fire disturbance on functional guild diversity over time using an experimental design.

Functional guilds assessed include: solitary ground nesters, social ground nesters, cavity nesters, cleptoparasites and *Bombus spp.* The main objectives of this study were to (1) assess overall bee community change and (2) determine the impact of fire over time by investigating the effect of fire on functional diversity of bees across various fire disturbance age categories in two oak savannah remnants in Southern Ontario. We also test the following specific hypotheses:

- 1). The proportional abundance of social and solitary ground nesters will increase immediately in habitat post fire disturbance. This hypothesis is predicted upon the findings that ground litter is eliminated and the amount of open ground for potential nesting sites is increased (Campbell *et al.*, 2007).

- 2). The proportional abundance of cavity nesters will decrease post fire disturbance as nesting substrate will ultimately be damaged and/or destroyed.

No predictions on how cleptoparasites or *Bombus spp.* will respond to fire were made. Not all host information is known for cleptoparasitic species, therefore predicting

how they will respond to fire disturbance is difficult. Nesting substrates differ among *Bombus* spp. therefore predicting how *Bombus* spp. as a group will respond is difficult.

3.3 Methods

3.3.1 Sample Sites

The habitat under investigation is oak savannah, which is a fire dependent habitat (Lavorel *et al.*, 2007) meaning that fire is required in order for its biodiversity and ecosystem function to be maintained (Whelan, 1995). Oak savannah in Southern Ontario is a very highly fragmented ecosystem but is thought to be a high quality habitat for bee species due to favorable nesting substrates (i.e., dry sandy soil for ground nesters, woody debris for cavity nesters), and a diverse flora providing ample food resources (Lee *et al.*, 1998). Two oak savannah remnants were chosen: Pinery Provincial Park (43° 16.691'N; 81°48.696'W) (henceforth Pinery), and Turkey Point Provincial Park (42° 42.117'N; 80° 20.262W) (henceforth Turkey Point).

Herein, a locality is defined as a provincial park, a site is defined as a burn area within a locality and a pan trap plot is defined as 30 pans separated 3m from each other within a site. Each locality consisted of various burn types: fresh burns (*fresh*) (< 3 years since fire at the end of the study), intermediate age burns (*intermediate*) (5-10 yrs since fire), mature burns (*mature*) (15-20 yrs since fire) and control (*control*) sites that have not

been burned, at least in 100 years. The *control* at Pinery was approximately 25 ha in size, while the control site at Turkey was 5 ha. The *fresh* burns at both localities occurred in the spring of 2008. At Pinery it was 60ha: the largest controlled low intensity fire to occur in the parks history; at Turkey Point it was 8 ha. There was no known burn history for *fresh* sites for the last 100 years at either locality. *Intermediate* sites at Pinery had been burned in 2000 whereas those at Turkey Point Park were burned in 2003. The *intermediate* site at Pinery was 50 ha in size that at Turkey Point was approximately 18 ha. *Mature* sites had been burned in 1993 and were approximately 50 ha and 15 ha in size respectively for Pinery and Turkey Point. Each sampling site was at least 0.20 km from the margin of a burn to minimize edge effects.

3.3.2. Bee Sampling and Identification

Pan traps were the chosen method of sampling because of their low-cost, simplicity, and ability to sample relative abundance and species richness of bees effectively and without collector bias (Bartholomew and Prowell, 2005; Campbell and Hanula, 2007; Kirk, 1984; Leong and Thorp, 1999; Westphal, 2007). Pan traps are also better than most methods for sampling cleptoparasitic species that are rarely found on floral resources (Roulston *et al.*, 2007; Sheffield *et al.*, 2012). This feature is particularly desirable as cleptoparasites are one of the first groups to respond after a fire (Moretti *et al.*, 2009).

Pan trap plots were in an X formation with bowls 3m apart with alternating pan colours- yellow, blue and white, following the protocol suggested by Droege *et al.*, (2003). To give replication, transects of 1km length had a total of 3-5 pan trap plots. Pan traps were set from 8:00h-17:00h each collecting day. Collecting took place every 10 days from May until September 2007-2010 to ensure that all species' flight periods were sampled. This provided 12 campaigns per year.

All specimens were identified to species level using various keys (Mitchell, 1960a & 1960b; Packer *et al.*, 2007). Other keys used for specific taxa were, Gibbs (2010) for metallic *Lasioglossum* spp.; McGinley, (1986) for *Lasioglossum sensu strictu*; Romankova (2003) for *Colletes* spp. and Lavery and Harder (1988) for *Bombus* spp. *Megachile* spp. and *Osmia* spp. collected in 2007 were initially verified by Dr. Cory Sheffield, *Bombus* spp were verified by Sheila. R. Colla. All specimens are currently housed at the York University Bee Collection (PCYU), Toronto, Ontario, Canada.

3.3.3 Bee Guilds

Bees were allocated into the following guilds for analysis: solitary ground nesters, social ground nesters, cavity nesters, bumblebees and cleptoparasites. Ground nesters were split into two guilds as social bee colonies can have many individuals per nest and solitary bees have only one (Gixti and Packer, 2008; Sheffield *et al.*, 2003; Williams *et al.*, 2010). **Solitary ground nesters** (e.g. *Agapostemon* Guerin-Meneville, *Andrena* Fabricus, *Colletes* Latreille, *Lasioglossum* Curtis (subgenus *Lasioglossum*), *Lasioglossum*

subgenera *Dialictus* Robertson, *Melissodes* Latreille, *Perdita* Smith, *Megachile latimanus* Say, *Megachile melanophaea* Smith), and **Social ground nesters** (e.g. *Lasioglossum* subgenera *Evyllaeus* Robertson, *Augochlorella* Sandhouse, *Halictus* Latreille) prefer open habitats, often those with dry sandy soils. **Cavity nesters** (e.g. *Augochlora pura*, *Heriades* Spinola, *Hoplitis* Klug, *Hylaeus* Fabricius, *Megachile* Latreille [other than species listed under solitary ground nesters above], *Osmia* Panzer, *Anthophora terminalis* Cresson, *Ceratina* Latreille) use pre-existing cavities such as pithy plant stems, rock cavities and abandoned beetle burrows in wood as nest sites (Cane *et al.*, 2007; Potts *et al.*, 2006). ***Bombus* spp.** were placed in a guild on their own, as they are social cavity nesters (Goulson *et al.*, 2008). **Cleptoparasites** (e.g. *Bombus* subgenus *Psithyrus* LePeletier; *B. ashtoni* (Cresson), *B. citrinus* (Smith), *Coelioxys* Latreille, *Epeolus* Latreille, *Nomada* Scopoli, *Sphecodes* Latreille, *Stelis* Panzer) are bees that lay their eggs in nests of their host species irrespective of host nest guild. We did not break cleptoparasites up into multiple guilds based upon host nest site choice because such data are not available for all species.

3.3.4 Statistical Analysis

For each fire site, data from pan trap plots were pooled prior to analysis as between pan colour differences were not the focus of the study.

To summarize the relationship between bee species richness and abundance for

each treatment within each locality, rank abundance plots were constructed (Magurran, 2004). This permitted us to assess if overall bee community structure was the same irrespective of guild membership among localities.

The methods put forth by Sheffield *et al.* (2013) were used to compare bee guild composition of different oak savannah successional ages- fresh, intermediate and mature burns and control. Species abundance data for each site were log transformed ($x = \log_2 n_i$) and fitted to a truncated lognormal distribution following Magurran (2004). The Lilliefors diagnostic was used to assess normality, as it is sensitive to departures from truncated log normality (Sokal and Rohlf, 1995) and previously used by Kevan *et al.* (1997) and Sheffield *et al.* (2013) for assessing normality of bee communities. This approach uses the Kolmogorov-Smirnov test for normality and if the test statistic D is less than P , then the sample is not significantly different from a lognormal distribution (Sokal and Rohlf, 1995).

Guild structure, as indicated above, was compared among localities and over time since disturbance to test if the temporal post fire patterns were the same among guilds. To test specific hypotheses indicated above, differences among guilds across collecting years in each treatment site, the proportional abundance of each guild was compared using a multiple comparisons test of proportions, $q_{0.05, 4} = 3.63$, following arcsine transformation, following Zar (1999). This transformation was chosen compared to other methods, as it is preferred for comparing small and/or large proportions (Zar, 1999).

3.4 Results

3.4.1 Community response

A total of 11 323 individuals were collected representing 225 species from all sites over 4 field seasons, from 2007 to 2010.

Rank abundance plots showed substantial variation in composition in *fresh* and *mature* among collecting years in Pinery while *control* and *intermediate* produced similar patterns across years (Figure 7).

Community structure at *control* and *fresh* at Turkey Point were similar to that of *control* and *fresh* at Pinery even though significantly fewer individuals were captured (Figure 8). *Intermediate* and *mature* at Turkey Point showed similar patterns across years, and dissimilar patterns of community structure from *intermediate* and *mature* at Pinery (Figure 8).

No samples from *control* at Pinery fit a lognormal distribution (Figures 9). The overall shape of the species distribution did, however, change among years: more species were observed in lower abundance octaves in 2007 compared to the later collecting years.

Mature at Pinery fit a lognormal distribution in 2008 ($D=0.0901$, $p=0.105$) and 2009 ($D=0.8031$, $p=0.1171$), but species composition in both years differed: more species were evident in higher abundance octaves in 2007 and 2008 compared to 2009 and 2010 (Figure 9). By 2010, the number of species had declined and there were more species in the lower abundance octaves.

Only 2009 fit a lognormal distribution at *intermediate* in Pinery ($D=0.0686$, $p=0.109$) where less species were observed in middle abundance octaves compared to lower and higher abundance octaves (Figure 9).

Fresh at Pinery fit a lognormal distribution in 2007 ($D=0.0726$, $p=0.901$) and 2009 ($D= 0.079$, $p= 0.109$) but not in other years. Fewer species were observed in 2008 compared to other collecting years. Fewer species were represented in middle abundance octaves at *fresh* in all years (Figure 9).

None of the site/year combinations at Turkey Point fit a truncated log normal distribution. For *control*, the shape of the species distribution changed considerably among years and very few species were collected in 2010 (Figure 10). For *mature*, the overall shape of the species distribution plot in 2007 was more similar to that of 2010 than for other collecting years. Species distributions for 2008 and 2009 were similar with more species being present in higher abundance octaves (Figure 10). At *intermediate*, species in higher abundance octaves were more predominant in 2009 and 2010 than in 2007 and 2008 (Figure 10). The number of species collected decreased over time at *fresh*, more species were present in higher abundance octaves in 2007 and 2009 compared to 2008 and 2010 where species only represented low abundance octaves (Figure 10).

3.4.2 Functional guild response

Below, all differences mentioned are statistically significant (Table 4 and 5).

Control at Pinery showed an increase in proportion of ground nesting bees in 2009, and in cleptoparasites over time, whereas the proportion of cavity nesters decreased in 2008 (Table 4).

The *mature* site showed increases in proportions of solitary and social ground nesters across years, an increase in cleptoparasites in 2009 and a decrease in cavity nesters from 2007 to 2009.

The proportion of cavity nesters in 2008 and cleptoparasites in 2009 increased at *intermediate* at Pinery whereas the proportion of solitary ground nesters decreased (Table 4).

In *fresh* at Pinery, the proportion of solitary ground nesters decreased over time, whereas social ground nesters, cleptoparasites, and *Bombus* spp. increased. Cavity nesters showed a strong increase in 2010 compared to other years (Table 4).

Turkey Point did not exhibit any significant differences in guild proportions among years at *control* and *intermediate* other than a decrease in solitary ground nesters and an increase in cleptoparasites in 2009 at *intermediate* (Table 5).

Mature at Turkey Point showed an increase in proportion of solitary ground nesters in 2008 and 2010 compared to 2007 and 2009 and a strong increase in cleptoparasites in 2009. No other significant changes were evident among guilds (Table 5).

At *fresh* in Turkey Point the only significant change was an increase in the proportion of cavity nesters in 2009.

3.5 Discussion

Previous work on the impact of fire on bee communities has demonstrated some differential impacts on different bee guilds (Potts *et al.*, 2003). However, these studies have looked at historical fires in an opportunistic manner without the benefit of pre-burn controls or experimental approaches. This study differs from previous work in having pre burn control data as well as experimentally planned burns. Furthermore, the timeline since fire covers 0-20 years, permitting assessment of immediate, short term and quite long term effects. Results show that different bee functional guilds respond differently to fire disturbance in oak savannah habitat.

3.5.1 Community response

Habitat that has been recently burned typically has lower bee diversity than nearby unburned habitat (Potts *et al.*, 2003). Community structure variations among burn treatments at both localities reflect this as composition in *fresh* sites showed low species diversity in 2008 (the sampling season immediately after a spring burn). Rank abundance plots showed that decreased bee diversity immediately post fire is longer lived than

studies have reported (Potts *et al.*, 2003) as bee community structure, in *fresh* at both localities was more similar to those at *intermediate* than to *control* sites (Figures 7 and 8).

Decreases in species richness and abundance from 2007 to 2010 in *mature* sites at both localities, provides further support for the role of intermediate levels of disturbance in maximizing bee diversity (submitted). Both *mature* sites had not seen fire in at least 15 years and bee community diversity was at its lowest in both localities at *mature* sites in 2010 with few abundant species and many represented by singletons compared to other collecting years. This shows that without the occasional fire, fewer species will be present (Figures 7 and 8).

Species abundance distributions such as the truncated lognormal can be used to model community health in natural ecosystems, where deviations from the models can be indicative of environmental perturbation of community structure (Hubbell, 2001; Kevan *et al.*, 1997; Magurran, 2007; Marcogliese, 2005; Sheffield *et al.*, 2013). Bee communities at Pinery fit the lognormal distribution in *mature* (2008), *fresh* (2007 and 2009) and *intermediate* (2009) suggesting that these sites may not have been suffering from environmental degradation during those years (Figure 9).

In contrast, the bee communities at Turkey Point showed no support for a lognormal distribution at any site for any year. This could result from the large number of hidden species that were predicted to occur in all sites at Turkey Point (Figure 10) as undetected species are known to alter fit to the lognormal distribution (Magurran, 2004). Some years at some sites at Pinery did show a lognormal distribution even though all sites for any year suggested higher numbers of undetected species compared to sites and

years at Turkey Point. Perhaps the support for the lognormal can be attributed to the fact that the total number of species exhibited (observed and hidden) was greater at Pinery than at Turkey Point (Figure 9 and 10).

Lognormal plots showed that a high proportion of rare species were captured across all burn treatments in both localities (Figure 9 and 10). A high proportion of rare species collected in previous works has been attributed to a variety of factors: insufficient sampling of habitats (Giles and Ascher, 2006), widespread rarity of species within communities (Sheffield *et al.*, 2013) or a high proportion of transient species (Williams *et al.*, 2001; Richards *et al.*, 2011).

The collecting methods used in this study are known to be adequate in sampling bees and have been used in numerous studies examining bee community change (Giles and Ascher, 2006; Grixti and Packer, 2006; Richards *et al.*, 2011; Romey *et al.*, 2007; Sheffield *et al.*, 2013). In this study, sampling consisted of 30 pan traps per pan trap plot. Turkey Point had 3 whereas Pinery had 5 pan trap plots per habitat type, for a total of 90 and 150 pan traps per habitat type at each locality respectively. Given the replicated sampling methodology across multiple years in this study, we believe that the high proportion of rare species is not associated with sampling and more indicative of community structure and/or transient species that could have been moving from an area whereas habitat structure was more suitable.

3.5.2 Functional diversity response

Fresh sites at both localities showed higher proportions of solitary ground nesters immediately post fire compared to bees of other guilds (Table 4 and 5). Post fire habitat would have a greater amount of open ground, which would support higher proportions of both solitary and social ground nesting species compared to ground not recently burned which would contain larger amounts of ground debris. This was also shown in the proportion of ground nesters found within *intermediate*, *mature* and *control* sites as the proportion of ground nesters decreased with time since fire (i.e. variation among your sample years, variation between sites or both). Our results agree with previous work that has shown that post fire habitat supports both solitary and social ground nesting species (Moretti et al., 2009; Ne'eman *et al.*, 2000; Potts *et al.*, 2005; Williams *et al.*, 2010).

Fire attributes such as intensity, seasonality and size can have a direct influence on bee functional diversity (Moretti *et al.*, 2009). Comparisons of bee community functional diversity in two diverse fire dependent ecosystems have shown that high fire intensity removes twig and stems suitable for bees that prefer preexisting cavities, whereas low intensity fires may not damage twig and stems that provide nest sites for cavity nesters such as *Ceratina* spp (Moretti *et al.*, 2009). Subsequently, size and location of nesting cavities in burn areas also influences bee functional guild response. Varying sizes of pieces of dead wood and stem location (above or in contact with flames) directly impact fuel loads, and thus fire intensity.

Our results agree with Moretti *et al.* (2009) as higher abundance of *Ceratina* spp. were found at Turkey Point where fire disturbance was small and of low intensity. Also, there was no significant change in the proportion of cavity nesters across sites at Turkey Point except for a significant increase immediately post fire (Table 5). Pinery burns however, were generally larger and more intense than those at Turkey Point, and did not show an increase in the proportion of cavity nesters over time for any treatment, in fact, there was a decrease over time within treatments (Table 1). Cavity nesting species collected in Pinery consisted mainly of *Osmia* spp., many of which prefer to nest in preexisting cavities of dead and damaged large pieces of wood that can be produced by intense fire (Cane *et al.*, 2007) and both the sites and the bees within may be expected to have a reasonable chance of surviving a fire *in situ*.

The vegetation community at Pinery has suffered from overgrazing by a dense population of white-tailed deer (*Odocoileus virginianus*) in past decades (Bazely *et al.*, 1997). A decline in the proportional abundance of cavity nesters could be associated with overgrazing of vegetation by deer; however, a decline in cavity nesters was also observed at Turkey Point where over browsing has not been problematic.

Floral resources will be minimal immediately post fire only for a short time period as fire often activates the seedbank and permits rapid recolonization of fire adapted floral species (e.g. Bond and Parr, 2010; Sugihara *et al.*, 2006). Studies examining the effects of fire on bee communities have shown that *Bombus* spp., tend to prefer habitats that are beyond an intermediate stage and resemble mature habitat (Potts *et al.*, 2003) compared to recently burned habitat.

A well-maintained oak savannah habitat contains many floral species (Lee *et al.*, 1998) and consequently should provide bee communities with abundant food resources. The relative proportional abundance of *Bombus* spp. at both localities was higher at *fresh* sites compared to *mature* sites, and the highest proportion of *Bombus* spp. collected was in 2010 at *fresh* in both localities (Table 1 and 2). As insects with an annual eusocial colony cycle, bumblebees need floral resources throughout the year and their populations may increase especially in recently burned areas following a few years of a flush in flowering. This result could be correlated to a more diverse a floral habitat heterogeneity produced within 2 years post fire rather than to one that has been established for 15-20 years (Hiers *et al.*, 2000).

Determining how cleptoparasites respond to fire disturbance is more challenging than examining changes among other functional guilds as host information is only known for very few cleptoparasitic species (Michener, 2007). That said, a stable and functional species community is one that is rich in species such as cleptoparasites and parasites that have the ability to radically change host population dynamics such as abundance and species richness (Hudson *et al.*, 2006; Marcogliese, 2005; Sheffield *et al.*, 2013).

Our results show that changes in the proportion of cleptoparasites across localities, over time and within fire treatments did not follow a pattern of recolonization as consistent as the other functional guilds did in each locality (Table 4 and 5). For instance, both localities showed a high proportion of cleptoparasites in the later collecting years across all burn treatments. Cleptoparasites could be moving into areas that resemble habitats that their host species (i.e., ground nesters) prefer, such as freshly

burned habitats. The increase in cleptoparasites in the established *mature* and *control* sites was due to high abundances of several species collected, as the majority of species collected were *Nomada* spp. which are known to be cleptoparasites on solitary ground nesters such as *Andrena* spp. that prefer open ground for nest sites.

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3. 8 Figures and Tables

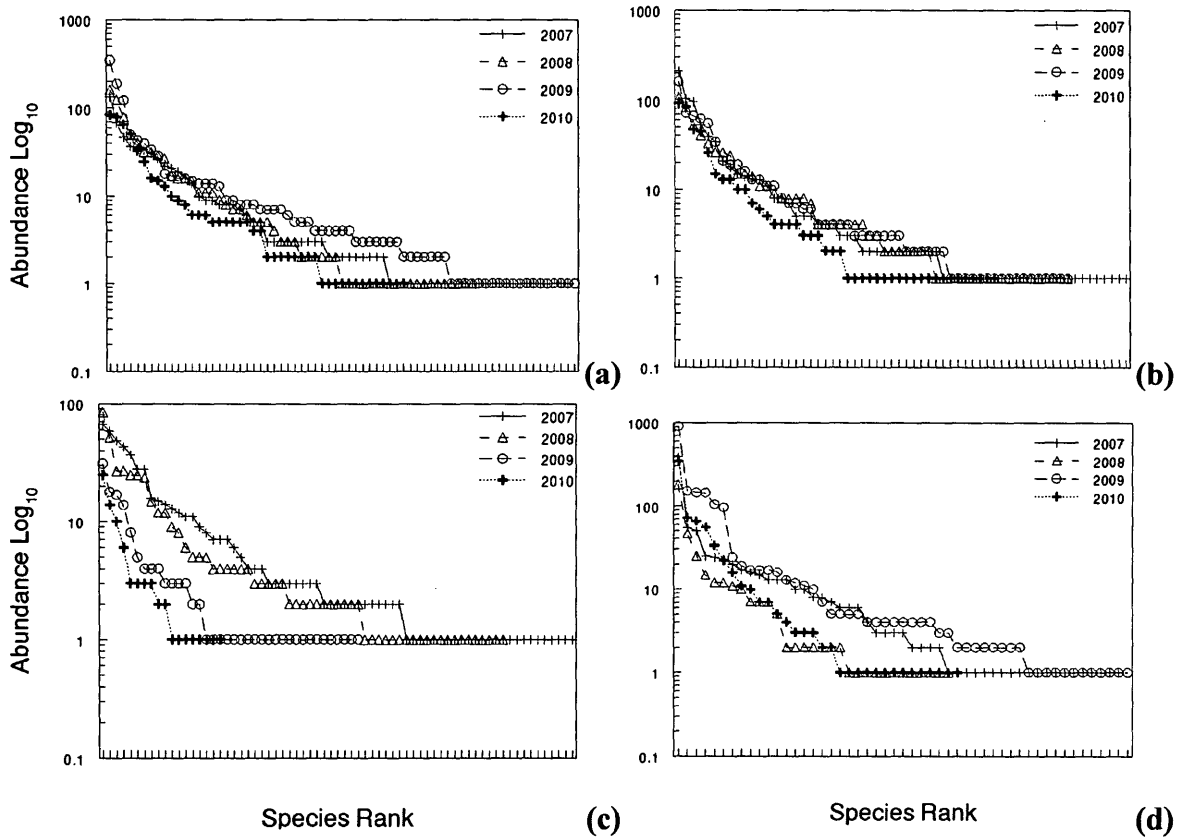


Figure 7- Rank abundance plots for all collecting years at (a) *control*, (b) *intermediate*, (c) *mature*, and (d) *fresh* at Pinery.

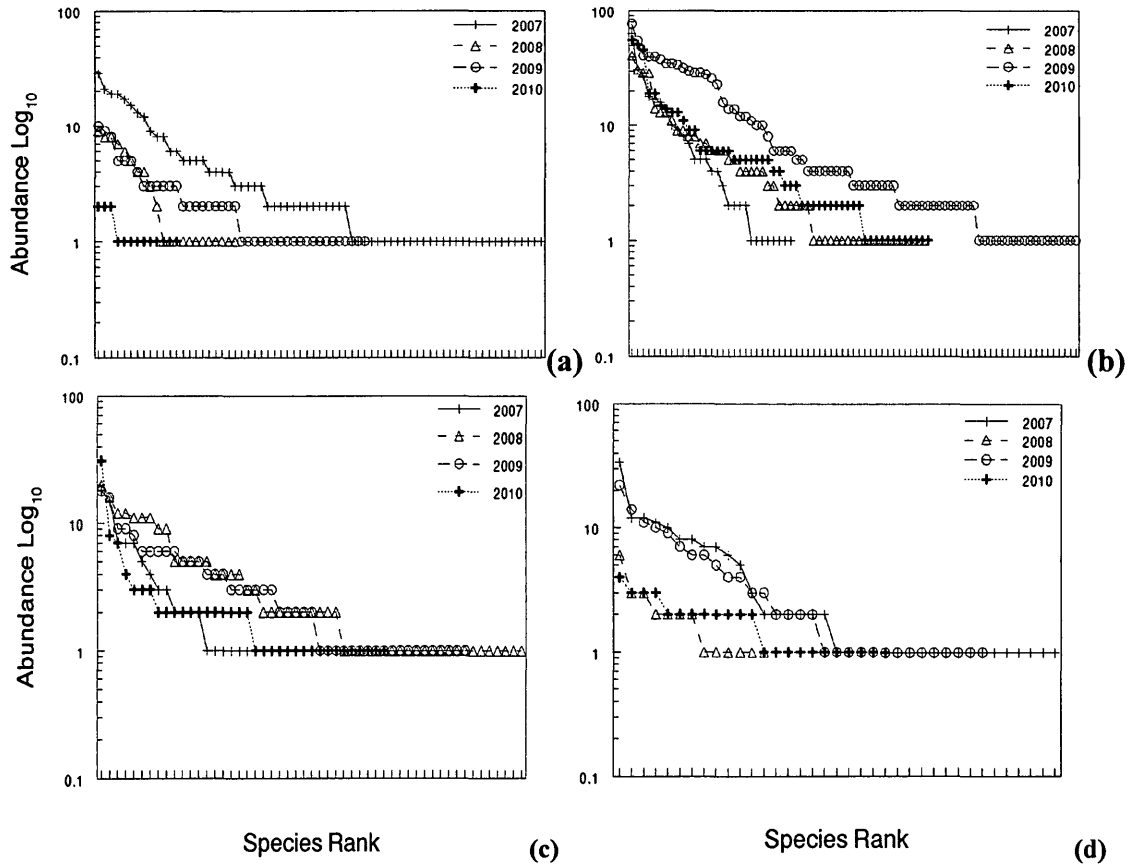


Figure 8- Rank abundance plots for all collecting years at (a) *control*, (b) *intermediate*, (c) *mature*, and (d) *fresh* at Turkey Point.

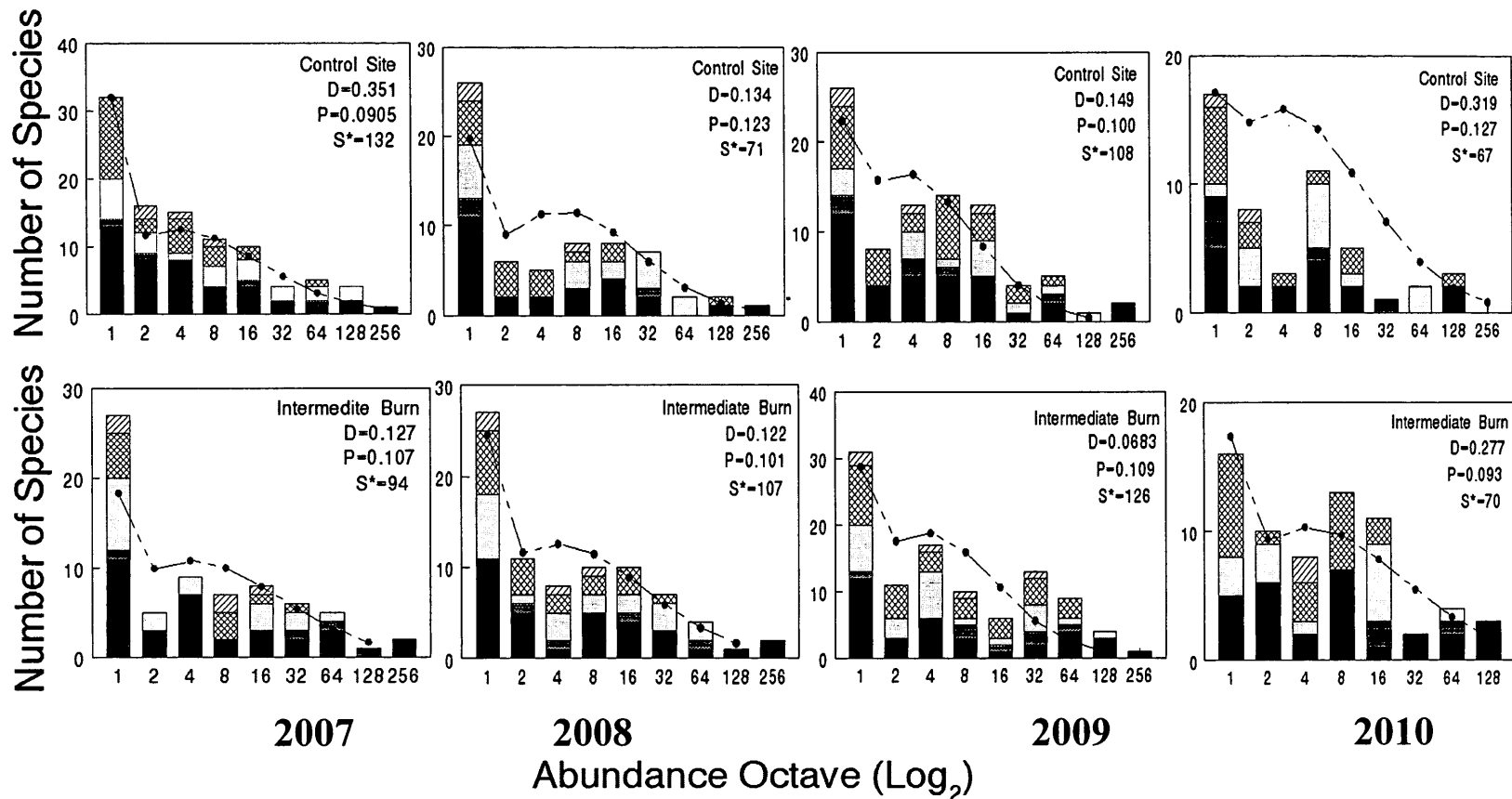


Figure 9- Proportion of bees found within guild plotted on a truncated lognormal distribution at *control*, *intermediate*, *mature* and *fresh* at Pinery for 2007-2010. Guilds are as follows: black= solitary ground nesters, dark grey= social ground nesters, light grey= cavity nesters, check= bumblebees, cross-hatching= cleptoparasites. When the test statistic D is less than P, samples show support for lognormal distribution. Kolmogorov-Smirnov test for normality with Lilliefors diagnostic only show support for a log normal distribution in *intermediate* in 2009.

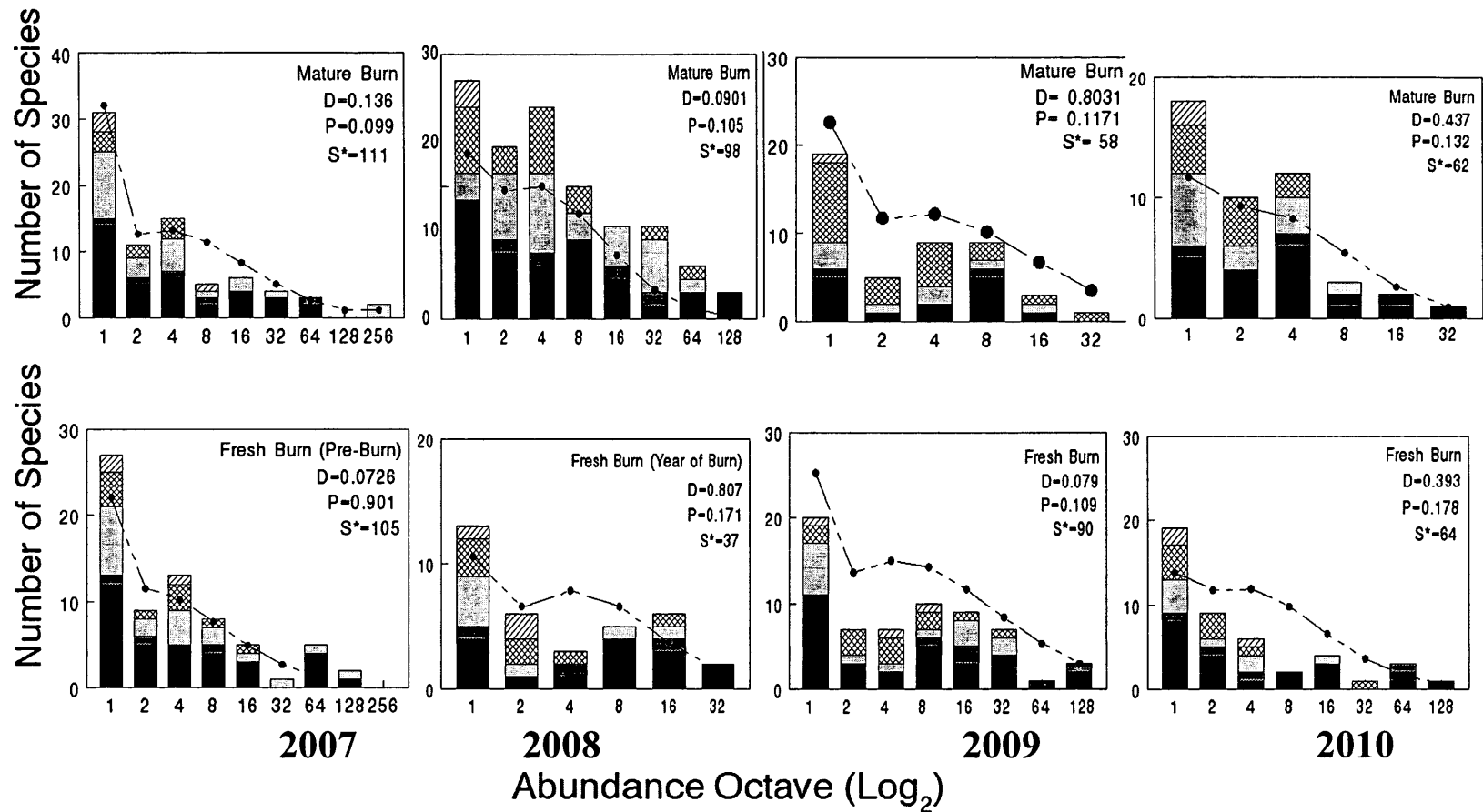


Figure 9 continued- Proportion of bees found within guild plotted on a truncated lognormal distribution at the *control*, *intermediate*, *mature* and *fresh* at Pinery for 2007-2010. Guilds are as follows: black= solitary ground nesters, dark grey= social ground nesters, light grey= cavity nesters, check= bumblebees, cross-hatching= cleptoparasites. When the test statistic D is less than P, samples show support for lognormal distribution. Kolmogorov-Smirnov test for normality with Lilliefors diagnostic only show support for a log normal distribution in the *intermediate* in 2009.

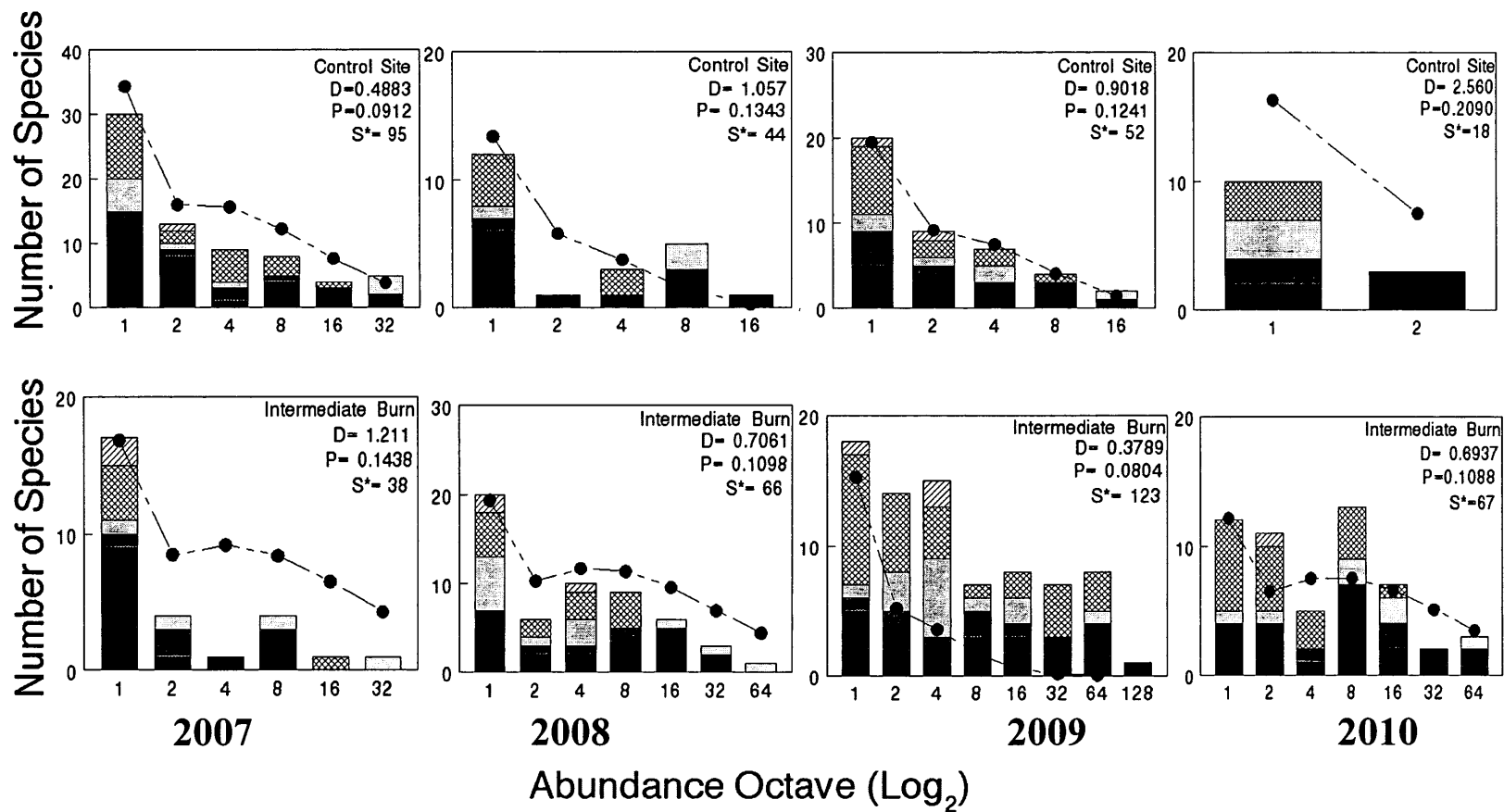


Figure 9- Proportion of bees found within guild plotted on a truncated lognormal distribution at the *control*, *intermediate*, *mature* and *freshet* Turkey Point for 2007-2010. Guilds are as follows: black= solitary ground nesters, dark grey= social ground nesters, light grey= cavity nesters, check= bumblebees, cross-hatching=cleptoparasites. When the test statistic D is less than P, samples show support for lognormal distribution . Kolmogorov-Smirnov test for normality with Lilliefors diagnostic did not show support for a log normal distribution in any burn sites across years.

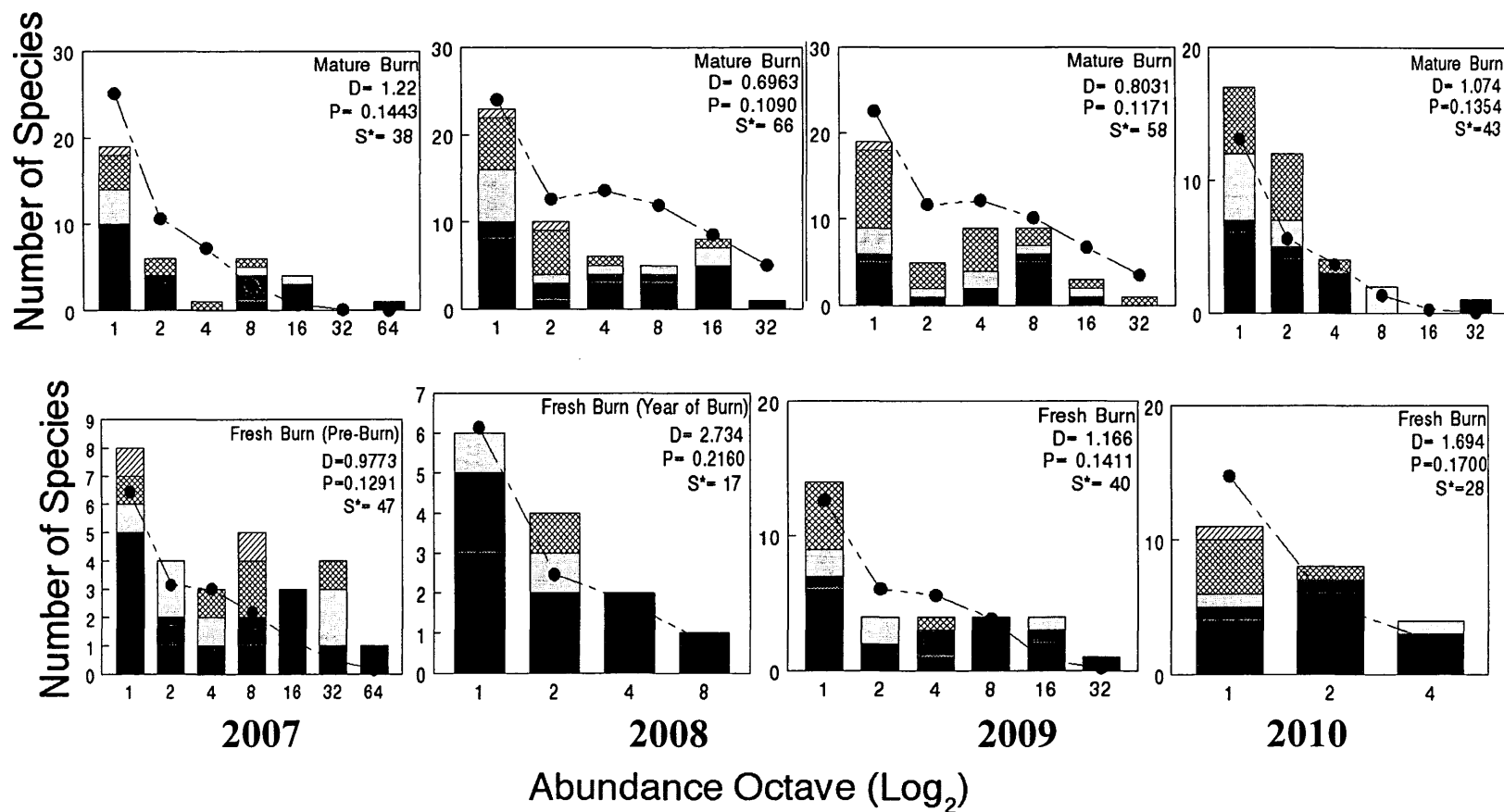


Figure 10 continued- Proportion of bees found within guild plotted on a truncated lognormal distribution at the *control*, *intermediate*, *mature* and *freshet* Turkey Point for 2007-2010. Guilds are as follows: black= solitary ground nesters, dark grey= social ground nesters, light grey= cavity nesters, check= bumblebees, cross-hatching= cleptoparasites. When the test statistic D is less than P, samples show support for lognormal distribution. Kolmogorov-Smirnov test for normality with Lilliefors diagnostic did not show support for a log normal distribution in any burn sites across years.

Table 4- Proportion of the total bee fauna representing each guild within each site from Pinery (non-transformed data). Results with different letters within each guild are significantly different (multiple comparisons of proportions, $q_{0.05, 4}=3.63$; after Zar 1999).

	Solitary Ground Nesters		Social Ground Nesters		Cavity Nesters		Cleptoparasites		<i>Bombus</i> spp.	
Control Site										
2007	0.48	(a)	0.04	(a)	0.36	(a)	0.10	(a)	0.01	(a)
2008	0.49	(a)	0.04	(a)	0.30	(b)	0.16	(b)	0.01	(a)
2009	0.58	(b)	0.05	(a)	0.22	(c)	0.13	(a)	0.02	(a)
2010	0.43	(a)	0.05	(a)	0.22	(c)	0.24	(c)	0.01	(a)
Intermediate Site										
2007	0.71	(a)	0.08	(a)	0.14	(a)	0.056	(a)	0.02	(a)
2008	0.55	(b)	0.07	(a)	0.27	(b)	0.096	(b)	0.01	(a)
2009	0.53	(b)	0.07	(a)	0.18	(abc)	0.21	(c)	0.02	(a)
2010	0.71	(a)	0.02	(b)	0.15	(ac)	0.11	(b)	0.01	(a)
Mature Site										
2007	0.45	(a)	0.04	(a)	0.39	(a)	0.10	(a)	0.02	(a)
2008	0.54	(b)	0.06	(a)	0.26	(b)	0.13	(a)	0.01	(a)
2009	0.40	(ac)	0.13	(b)	0.15	(c)	0.32	(b)	0.003	(a)
2010	0.59	(bd)	0.15	(b)	0.15	(c)	0.10	(a)	0.01	(a)
Fresh Site										
2007	0.61	(a)	0.11	(a)	0.22	(a)	0.05	(a)	0.01	(a)
2008	0.68	(ab)	0.08	(a)	0.12	(b)	0.11	(b)	0.02	(ab)
2009	0.67	(b)	0.17	(b)	0.09	(b)	0.06	(a)	0.01	(a)
2010	0.47	(c)	0.19	(b)	0.64	(c)	0.19	(c)	0.06	(b)

Table 5- Proportion of the total bee fauna representing each guild within each site from Turkey Point (non-transformed data). Results with different letters within each guild are significantly different (multiple comparisons of proportions, $q_{0.05, 4}=3.63$; after Zar 1999).

	Solitary Ground Nesters		Social Ground Nesters		Cavity Nesters		Cleptoparasites		<i>Bombus</i> spp.	
Control Site										
2007	0.47	(a)	0.05	(a)	0.26	(a)	0.21	(a)	0.01	(a)
2008	0.61	(a)	0.15	(a)	0.21	(a)	0.16	(a)	0	(b)
2009	0.48	(a)	0.06	(a)	0.20	(a)	0.24	(a)	0.03	(a)
2010	0.50	(a)	0.13	(a)	0.19	(a)	0.19	(a)	0	(b)
Intermediate Site										
2007	0.55	(a)	0.04	(a)	0.22	(a)	0.17	(a)	0.02	(a)
2008	0.52	(a)	0.04	(a)	0.28	(a)	0.14	(a)	0.02	(a)
2009	0.40	(b)	0.04	(a)	0.22	(a)	0.33	(b)	0.01	(a)
2010	0.55	(a)	0.07	(a)	0.22	(a)	0.15	(a)	0.01	(a)
Mature Site										
2007	0.39	(a)	0.10	(a)	0.29	(a)	0.20	(a)	0.02	(a)
2008	0.54	(b)	0.07	(a)	0.20	(a)	0.18	(a)	0.02	(a)
2009	0.32	(a)	0.04	(a)	0.16	(a)	0.47	(b)	0.01	(a)
2010	0.55	(b)	0.03	(a)	0.24	(a)	0.18	(a)	0	(a)
Fresh Site										
2007	0.60	(a)	0.10	(a)	0.16	(a)	0.13	(a)	0.01	(a)
2008	0.50	(a)	0.08	(a)	0.35	(b)	0.08	(a)	0	(b)
2009	0.67	(a)	0.13	(a)	0.13	(a)	0.06	(a)	0	(b)
2010	0.65	(a)	0.08	(a)	0.10	(a)	0.15	(a)	0.03	(a)

Chapter 4- Estimating bee species occupancy in oak savannah habitat of Southern
Ontario Canada

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4.1 Abstract

Recent reports of global bee species decline have highlighted the need for more thorough monitoring programs to determine bee species occurrence and persistence over time. Equally important to reporting on bee species occupancy is assessing species responses to environmental disturbances. In this study, data from the 12 most common bee species captured in two oak savannah habitats in Southern Ontario were used to test whether bees within a nesting guild have similar patterns of occupancy among sites in the same fire category. Overall this study agrees with published studies that have shown fire disturbance to be an important for bee species. Frequently bee biodiversity studies employ functional guilds to examine how environmental disturbance effect bee communities. However, it is unclear whether or not species of the same functional guild respond similarly to the same environmental disturbance. It has been demonstrated that many species belonging to the same functional guild may have intraspecific traits that result in variation in occupancy across fire disturbed habitat. Though the use of functional guilds can indisputably reveal bee community change in a more precise manner than overall biodiversity statistics, our results strongly emphasize the importance of assessing the response of individual species: bee species within guilds showed different responses to burned habitat of different ages.

4.2 Introduction

Whether or not a species is present in a set of habitat units is a fundamental concept in ecology and is an essential parameter for conservation biology (Krebs, 1999). The status of a species in a locality or area is usually assessed based on count data which are then used to estimate relative abundance and other community diversity parameters (e.g. Bailey *et al.*, 2004). When multiple sites are sampled, it is possible to quantify the proportion of sites where a species was found (Bailey *et al.*, 2004; Pilliod and Peterson, 2001). However, there are numerous reasons why a species may exist at a sample site but not be detected. Being able to assess the preponderance of such false absences is essential, especially for conservation biology and restoration ecology. Species occupancy (Ψ) is the proportion of area, patches, or sample units that are occupied by a species, whether they were actually detected in surveys or not (MacKenzie *et al.*, 2005). Species detection probability (p) is the probability of detecting at least one individual of a species during a sampling period, given that individuals of the species are present in (i.e. they occupy) the habitat (MacKenzie *et al.*, 2002). In any given survey a species can be detected, requiring occupancy, $\Psi \times p$, or not detected, which can indicate the species is present but was not detected in the survey, $\Psi \times (1 - p)$, or the species is not present $1 - \Psi$.

Statistical models have been employed to examine situations in which species detection is less than one and where detectability varies among species (MacKenzie *et al.*, 2002). The models use the proportion of area (or sampling units) occupied to determine the species status. They require that the sample sites be visited multiple times

within the detectable period for the species being assessed; this will depend, for example, upon the species' phenology (MacKenzie *et al.*, 2002). In this study, the organisms of interest are bees, which as a group are active from spring to fall, although the proportion of all species that can be detected at any time during this extended period may be small (Richards *et al.*, 2011).

Bees are a vital component of most terrestrial ecosystems due to the pollination services they provide (Biesmeijer *et al.*, 2006; Breeze *et al.*, 2011). Recent studies have reported bee declines in ecosystems around the world (Biesmeijer *et al.*, 2006; Burkle *et al.*, 2013). Regions where bee declines and changes in diversity have been reported have had large scale monitoring programs implemented for many years to draw upon for analysis (Winfree, 2010).

One approach to quantifying bee decline and showing changes in diversity over time is the use of functional guilds (Grixti and Packer, 2006; Williams *et al.*, 2010). A functional guild is a group of organisms with similar ecological, behavioural or life history traits (Tilman and Lehman, 2001). The use of functional guilds in examining community change allows researchers to determine how groups of organisms function in the face of and/or respond to environmental perturbation. In this study, bees were grouped into guilds based on their nesting requirements, the perturbation was experimentally controlled fire and the habitat was oak savannah in southern Ontario. Guilds and the species analyzed from within them (see below for rationale for species inclusion in the analyses) were: solitary ground nesters (*Agapostemon splendens* Lepeletier, *Andrena miranda*, Smith and *Lasioglossum acuminatum* McGinley, *L.*

coriaceum Smith, *L. leucozonium* Schrank, *L. pilosum* Smith); social ground nesters (*Augochlorella aurata* Sandhouse, *Bombus impatiens* Cresson); cavity nesters (*Ceratina dupla* Say, *Lasioglossum cressonii* Robertson), and cleptoparasites (*Nomada maculata* Cresson, *Nomada* sp. 1).

Oak savannah is a fire dependent habitat with both meadow and forest assemblages (Lee *et al.*, 1998). In recent years, fire dependent habitats have been shown to be of great importance to bee species because of their diverse flora and nesting resource availability (Noel *et al.*, 2007; Taylor and Catling, 2011).

Here we examine the proportion of area occupied and the probability of detecting the 12 most common bee species captured in 4 different fire categories at two prime oak savannah habitats in Southern Ontario, Canada. This is the first application of occupancy models to data on bees. Furthermore, it is the first study of occupancy for any taxon using experimentally modified habitats with fire as the disturbance across multiple seasons to test how individual species respond to fire. We test the following hypotheses:

1). That bees within a nesting guild have similar patterns of occupancy among sites in the same fire category. If fire history impacts bees of the same guild similarly, then their occupancy in sites with the same fire history should be similar. This hypothesis is fundamental to the use of guilds, rather than overall biodiversity statistics in ecological response studies; however, it has not yet been rigorously tested.

2). That ground-nesting bees have higher occupancy 1-3 years after a fire. This hypothesis is predicated upon the findings that ground-nesting bees seem to become more abundant soon after a fire (Ne'eman *et al.*, 2000; Potts *et al.*, 2005; Williams *et al.*, 2010)

presumably, because ground litter is eliminated and the amount of open ground for potential nesting sites is increased (Campbell *et al.*, 2007).

3). That cavity-nesting bees have decreased occupancy soon after a fire (Morretti *et al.*, 2009; Williams *et al.*, 2010). This is certainly expected because the stems and wood that cavity-nesting bees use as nesting substrate would have been burned and this nesting resource will not have had time to regenerate soon after a fire.

4.3 Methods

4.3.1 Study Sites and Fire History

Pinery Provincial Park (N43° 15.317' W081° 49.739') (henceforth Pinery) is arguably the largest intact oak savannah remnant in North America (McKenzie, pers com). It occupies approximately 2 532 ha and is located on the east shore of Lake Huron. Turkey Point Provincial Park (N42° 42.247' W080 19.689') (henceforth Turkey Point) was established in 1959 and is located on the north shore of Lake Erie. For detailed descriptions of these locations see Lee *et al.*, (1998).

In this study, a locality is defined as a provincial park, and a sample site is defined as a burn area within a locality. Each locality consisted of four burn categories: fresh burns (*fresh*) (< 2 years, this category is considered to be “soon” after a fire for purposes of testing hypotheses 2 and 3 above), intermediate age burns (*intermediate*) (5-10 yrs), mature burns (*mature*) (15-25 yrs) and control (*control*) sites that have not been burned for at least 100 years. Please see table 7 for year of burn and size of each fire category

site at each locality. Each sampling site was approximately 0.3 km within a burn type to control for edge effects.

4.3.2 Bee Sampling and Identification

Pan traps were the chosen method of sampling because of their low-cost, simplicity, and ability to effectively sample relative abundance and species richness of bees in a repeatable manner (Bartholomew *et al.*, 2005; Campbell *et al.*, 2007; Westphal *et al.*, 2008). Pan traps are also better at sampling cleptoparasitic species that are rarely found on floral resources (Roulston *et al.*, 2007). This feature of pans is extremely desirable for this study as recent studies on fire and bees have shown that cleptoparasitic species are one of the first groups to respond after a fire (Moretti *et al.*, 2009; Sheffield *et al.*, 2013).

A pan trap plot is defined as 30 pans in an X formation with bowls 3m apart with alternating colours- yellow, blue and white, following the sampling protocol of Droege *et al.*, (2003). Transects of 1km length had a total of 3-5 plots to give replication within each transect. Pan traps were set from 8:00h-17:00h each collecting day. Collecting took place every 10 days from May until September 2007-2010 to ensure that all species' flight periods were sampled resulting in a total of 7-10 surveys per year depending on weather.

All specimens were identified to species level using various keys (Mitchell 1960a & b; Packer *et al.* 2007; Polistes Corporation 2007). Other keys used for specific taxa

were, Gibbs (2010) for metallic *Lasioglossum* spp.; McGinley (1986) for *Lasioglossum sensu strictu*; Lavery and Harder (1988) for *Bombus* spp. *Bombus* spp were verified by Dr. Sheila. R. Colla. All specimens are housed at the York University Bee Collection (PCYU), Toronto, Ontario, Canada.

4.3.3 Statistical Methods

Following Potts *et al.*, (2006), species chosen for inclusion in the analysis each represented at least 0.5% of the total number of individuals collected. The 12 most common bee species are shown in table 1 and 2. We followed Mackenzie *et al.*'s, (2002) likelihood-based method for estimating the proportion of species occupying sample sites when species detection probabilities are less than one. This method is based on closed population capture-recapture theory and has three principle assumptions: (1) the community is closed to additions from other habitats (2) individuals are correctly assigned to species-level units and (3) the probability of detecting one species at a site is independent of the probability of detecting the same species at all other sites. We assess the extent to which these assumptions were met and the importance of adequate sampling in the discussion.

All modelling was completed using PRESENCE software (Hines, 2006) with fire as a covariate defined as site, in all models. To test the specific hypotheses stated above, single year models were employed for all 12 species for each of the 4 collecting years.

The first model held both the proportion of sites occupied and species detection constant, $\Psi(\cdot)p(\cdot)$; subsequent models were executed by varying covariates of Ψ and p to determine which model was the best representation of the data. Both Ψ and p expressed as logit functions with site-specific covariates (i.e. fire category “site” and year). The models examined and their corresponding AIC values (Akaike, 1973) are shown in table 8. The model that produced the lowest AIC value was with Ψ and p defined independently for each year and was used in each subsequent analysis (Table 8). Models in the analyses may not be the models that fully describe what influences bee species occupancy and species detection in burn site categories at both localities, however, they were chosen based on the hypotheses to be tested and not *a posteriori*.

4.4 Results

4.4.1 Data Summaries

Over 4 field seasons, from 2007 to 2010, we collected 11 323 individuals representing 225 species of bees from a control and 3 burn sites at each of our 2 localities. There were 7110 individuals collected of the 12 most common species that were used in occupancy analyses, including representatives of the 4 different nesting guilds noted above.

In the following, we first describe the statistically significant and strongest patterns for each species, guild by guild, before assessing the extent to which the predictions of the hypotheses are supported by the data.

Agapostemon splendens showed significant decline in *mature* and *fresh* followed by gradual recovery at Pinery whereas an extreme decline in *mature* and a delayed decline in *control* was observed at Turkey Point (Figure 11a).

Occupancy estimates for *An. miranda* showed a significant immediate decline at *fresh* and a significant increase followed by an increased in occupancy in *mature* at Pinery. Significant increases in occupancy were found for this species at all sites at Turkey Point in 2008 with the exception of *fresh* (Figure 11b).

Lasioglossum acuminatum exhibited a significant decrease in *mature* in 2010 at Pinery, whereas all burn sites except for *fresh*, showed decreases in occupancy in the last year at Turkey Point (Figure 11c).

For *L. coriaceum* there were declines in 2008 across burn sites over time at Pinery and a decline in *fresh* 2 years after fire at Turkey Point (Figure 11d).

Occupancy estimates for *L. leucozonium* increased in 2008 followed by a decrease in all sites except for *intermediate* at Pinery. All sites but *intermediate* showed declines in occupancy for this species by 2009 at Turkey Point although both *mature* and *fresh* had increased occupancy in 2010 (Figure 11e).

Lasioglossum pilosum showed a significant decrease followed by a significant increase in *mature* and an increase in occupancy across *control* and *fresh* at Pinery. Occupancy estimates for *L. pilosum* decreased in 2009 at all sites but *fresh* at Turkey

Point, the *control* recovered in 2010 whereas *mature* and *intermediate* site continued to decline (Figure 11f).

Social ground nester *Au. aurata* decreased in occupancy in *control* and *fresh* in 2009, and decreased in 2010 in *mature* at Pinery (Figure 9a). Occupancy estimates for *Au. aurata* at Turkey Point revealed a significant increase in *fresh* in 2008, and a significant decline in 2009 followed by an increase in occupancy at all three other sites (Figure 12a).

Bombus impatiens showed significant decreases in *fresh* and *mature* in 2009 and increased in 2010 at Pinery. Gradual declines were observed in occupancy in all sites but *fresh* at Turkey Point whereas occupancy significantly increased in 2009 followed by a decline to zero at all sites in 2010 (Figure 12b).

Ceratina dupla showed declines in occupancy across all sites at Pinery and declines at most at Turkey Point. The exceptions were for *intermediate*, where there was no change in occupancy and an increase in occupancy at *mature* in 2010. However, declines were delayed until 2010 at *fresh* (Figure 13a).

Occupancy estimates for *L. cressonii* showed declines in 2009 at Pinery at all sites except *control*, although *fresh* increased prior to the decline. *Lasioglossum cressonii* showed a significant increase in 2008 followed by a decrease at *mature*, where at *control* it decreased significantly in 2010 at Turkey Point (Figure 13b).

Nomada maculata showed strong declines in *control* and *intermediate* in 2008 followed by recoveries at Pinery while declines continued to 2009 at *mature* which increased in 2010. Occupancy for *N. maculata* in *intermediate* and *mature* at Turkey

Point significantly increased in 2008, declined significantly in 2009 followed by recovery in 2010 at all sites (Figure 14a).

Nomadasp.1 showed increases in occupancy at all sites in 2008 which continued until 2009 at *fresh* and *intermediate*. The *mature* showed a dramatic decline compared to other sites at Pinery. Occupancy estimates at Turkey Point exhibited significant declines and increased in occupancy across all sites in different years (Figure 14b).

4.4.2 Tests of the Hypotheses

Results for solitary ground nesting species *An. miranda* at both localities, *L. acuminatum* at Pinery, *L. coriaceum* at Turkey Point, *L. leucozonium* at both localities, and *L. pilosum* at Pinery showed limited support for hypothesis 1 (bees within a nesting guild have similar patterns of occupancy among sites in the same fire category): occupancy at *intermediate* showed the same pattern (Figure 11b-f). However, there was no support for hypothesis 1 at *control*, *fresh* or *mature* among solitary ground nesters because of variable responses among members of this guild (Figure 11a-f).

Eusocial species also showed limited support for hypothesis 1 as *Au. aurata* at Turkey Point and *B. impatiens* at Pinery showed similar patterns of occupancy only at *control*, and *mature* (Figure 12a and b). No similar patterns of occupancy were evident among other fire categories for *Au. aurata* and *B. impatiens*.

There was no support for hypothesis 1 among cavity nesters at fire category sites as different patterns of occupancy were evident at both localities (Figure 13a and b).

Cleptoparasitic species at both localities showed limited support for hypothesis 1 with similar patterns in occupancy only in *fresh* sites immediately after the burn with the exception of *N. maculata* at Turkey Point whereas occupancy did not change from 2007 to 2008 (Figure 14).

Lasioglossum leucozonium, and *L. pilosum* at Pinery were the only solitary ground nesters to show marginal support for hypothesis 2 (ground nesting bees have higher occupancy post fire) with increases in occupancy at the *fresh* post fire in 2008 (Figure 11e and 11f).

There was very limited support for hypothesis 3 (cavity nesting bees have lower occupancy post fire), as only occupancy for *C. dupla* declined after fire and then only at Pinery (Figure 12a).

4.5 Discussion

Here, we first assess the extent to which our study sites and design meet the assumptions of occupancy models and then we discuss the extent to which our hypotheses are supported by the results.

Sampling design plays an essential role in biodiversity surveys. Without proper attention to design, conclusions regarding species status can be misleading (Polluck *et al.*, 2002). In this study, 7110 individuals of our 12 focal species were sampled at least 7 times over each of 4 field seasons (2007-2010) in control sites and fire disturbed habitats of three different ages that had been experimentally burned as recently as 2008. Conducting only 1 or 2 sampling occasions per season can greatly underestimate occupancy due to temporal and spatial variation in species abundance (Bailey *et al.*, 2004; MacKenzie *et al.*, 2005). Not all bee species are active for a substantial proportion of our sampling periods. We would expect occupancy results to be more true for species which are active for longer periods of time as they are expected to be present for a larger number of sampling occasions. The 12 species in our analyses, ranked in duration of flight activity longer flight to shorter flight periods are as follows: social bees are active for longer periods than solitary bees, solitary halictids and *C. dupla* are active longer than *An. miranda* and *Nomada* spp.. This sequence is based on known phenologies of the 12 species examined (Richards *et al.*, 2011). Results however, show that data are not more accurate for species which are active for longer periods and do not explain the differences in occupancy estimates between our predictions and observations.

Though *B. impatiens* and *Au. aurata* are members of the same nesting guild and are active for most of the entire bee flight season, they only showed similar occupancy pattern estimates in two of 8 possible site/location combinations (*control*, and *mature* sites at Pinery (Figure 12a and b)).

The principle assumptions outlined above were met in the study as: (1) the communities were largely closed to additions from other habitats as both localities are surrounded by farmland and water: lake Huron to the North of Pinery and lake Erie to the south of Turkey Point; (2) we believe the species used in the analyses were correctly identified as representative vouchers were verified by experts; (3) food and nesting resources determine which bee species can be found at a site, as these varied among sites (Lee *et al.*, 1998), the probability of detecting a species at one site was independent of the probability of detecting the same species at other sites.

Though each locality was closed with respect to proximity to similar habitats, Turkey Point is a smaller area than Pinery and the fire sites there were closer to each other. A plausible explanation for variation in species-specific occupancy between localities could be due to differences in the extent of independence among fire sites due to closer proximities among them at Turkey Point. This would be expected to influence smaller bees more than larger ones because they have shorter foraging and dispersal distances (Osborne *et al.*, 2008; Zurbuchen *et al.*, 2010). However, simple inspection of figures 8-10 indicates that the smaller bees (*Au. aurata*, *C. dupla*, *L. cressonii*, and *L. pilosum*) are not less variable among the Turkey Point sites than at Pinery.

Occupancy methods were only used for the 12 most common bee species found at both localities. The methods used in this study might not be useful in determining occupancy of rare bee species as detection is expected to be quite low and it is thought that a species should be found in 15% of the surveys if occupancy models are to be considered accurate (Bailey *et al.*, 2004).

Even though results show variation in species-specific occupancy, they do suggest some consistent patterns with respect to bees' temporal responses to fire. Evidence for this comes from support for hypothesis 1 where solitary ground nesters: *An. miranda* at both localities, *L. acuminatum* at Pinery, *L. coriaceum* at Turkey Point, *L. leucozonium* at both localities, and *L. pilosum* at Pinery all showed an occupancy probability of 1 in all years at *intermediate* sites (Figure 11). An occupancy probability of 1, with no change over time, suggests that bee diversity is maintained in fire dependent habitats with disturbance over an intermediate time. *Andrena miranda*, *L. acuminatum* and *L. pilosum* at *fresh* at Turkey Point were the only species to also show an occupancy probability of 1, with no change over time at other sites. This agrees with studies that have shown that bee diversity is at its highest 5-10 years post fire (Moretti *et al.*, 2009; Pindar, 2013; Potts *et al.*, 2003; Potts *et al.*, 2006).

Both cleptoparasitic species occupied post fire more than pre fire habitats with the exception of *N. maculata* at Turkey Point (Figure 14a). This result also supports the hypothesis that bees within a guild have similar occupancy among sites with the same fire category and agrees with other studies that have shown that cleptoparasitic species are the

first to move into newly disturbed habitat as the habitat now contains more possible nesting sites for their hosts (Pindar, 2013).

Occupancy results showed very limited support for the hypothesis that ground-nesting bees have higher occupancy soon after a fire (Figure 11). Only *L. leucozonium* and *L. pilosum* at Pinery showed higher occupancy post fire (Figures 11e and f). This result was not expected as previous studies have shown that ground nesting species are more abundant in habitats that have been burned (Moretti *et al.*, 2009; Williams *et al.*, 2010). Even though most ground nesting species prefer to nest in open ground it is known that some prefer to nest immediately beneath the rosettes of low-growing plants (Packer and Knerer, 1986). This amount of natural historical detail is not known for many species and it was not possible to assess whether any species preferred bare soil over patchily vegetated ground. However, if some species prefer particular vegetation densities, as seems probable, this could explain the high variation in occupancy among the ground nesting species examined herein (Figure 11).

Results for *C. dupla* support the hypothesis that cavity nesting bees decrease in occupancy after a fire whereas data for *L. cressonii* did not support it (Figure 13). *Ceratina dupla* is known to nest in pithy stems (Rehan and Richards, 2010) which would have been burned in a recent fire. *Lasioglossum cressonii* nests in rotten wood (Mitchell, 1961) and results from Pinery show that it prefers to occupy habitat more recently burned compared to other fire category sites (Figure 13b). Recent fire disturbance at Pinery may have exposed more deadfall and provided more suitable nesting sites for *L. cressonii*, thereby offering a plausible explanation for this species' increasing occupancy after a

fire. This further supports the need for detailed natural historical data in that different cavity nesting species may respond differently to fire depending upon the details of the particular cavities they prefer to nest in.

4.6 Conclusion

Many studies have shown the importance of incorporating functional guilds into biodiversity studies in providing additional insight on how environmental disturbances influence community responses (Grixti and Packer, 2006; Tilman and Lehman, 2001; Scorsati *et al.*, 2011; Williams *et al.*, 2010). However, this study demonstrates the need for more thorough assessment of the ecology of individual species within functional guilds. This is because species occupancy within habitats, and species responses to environmental disturbances varied substantially within guilds. It seems likely that nest-site divisions currently employed in guild-based biodiversity assessments are likely too coarse. Whether a ground-nesting bee prefers entirely bare ground, sparsely vegetated soil, densely vegetated ground or will nest only beneath the basal leaf rosettes of particular plant will all influence its response to disturbance. Similarly, while pithy stems will be entirely removed from a burned site, bees that nest in above ground cavities in large pieces of dead wood might benefit from a recent fire.

4.8 References

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4.7 Figures and Tables

Table 6- Fire history and size of sites and Pinery and Turkey Point Provincial Park.

Fire category	Locality			
	Pinery (ha)	Burn Year	Turkey Point (ha)	Burn Year
Control (unburnt)	25	N/A	5	N/A
Fresh fire (0-2 yrs)	60	2008	10	2008
Intermediate fire (5-10 yrs)	50	2000	18	2003
Mature fire (15-25yrs)	50	1993	15	1993

Table 7- Models explored using PRESENCE software (Hines, 2006) and their AIC values, delta AIC, Number of parameters and -2*LogLike results.

Model	AIC value	deltaAIC	Number of parameters	2*LogLike
$\Psi(\text{site}),p(\text{site})$	27.26	0	6	15.26
$\Psi(\cdot),p(\cdot)$	32.61	5.35	8	16.61
$\Psi(\text{year}),p(\text{year})$	58.01	30.75	9	40.01

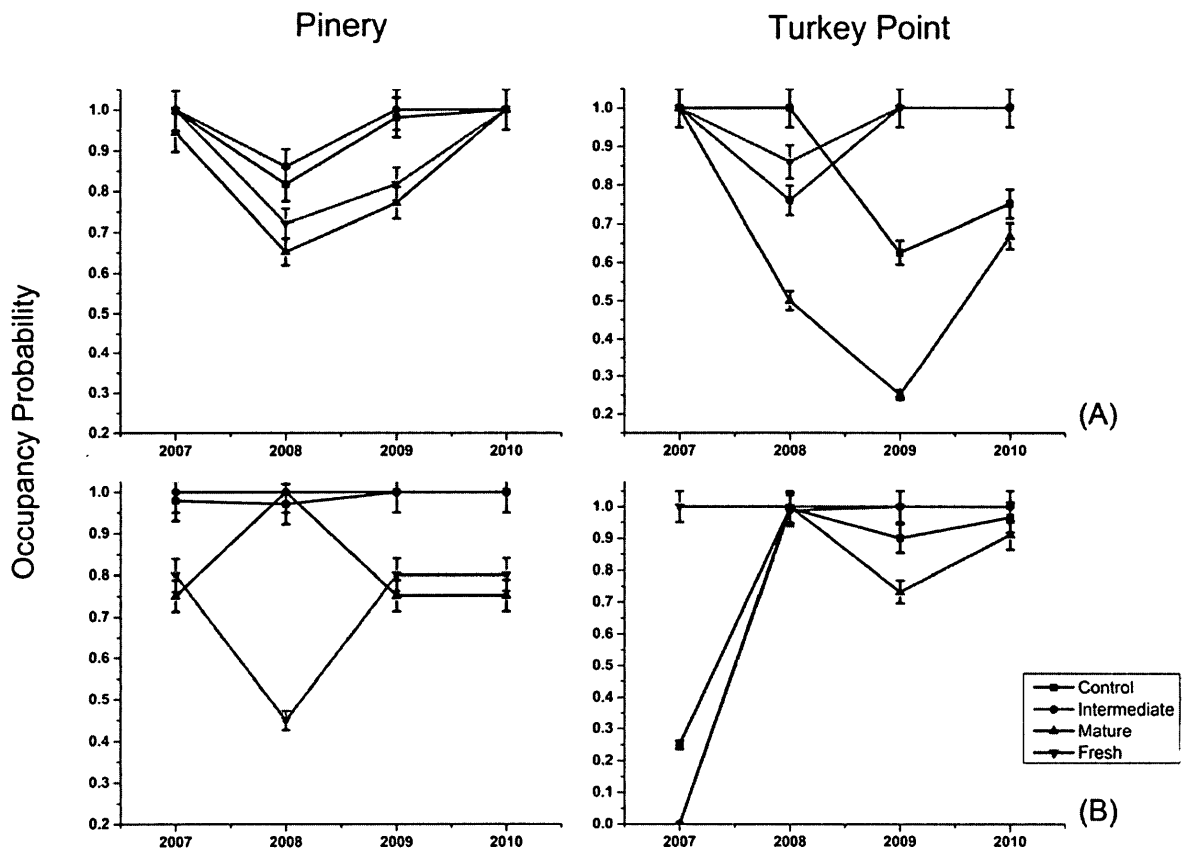


Figure 11- Occupancy probabilities and variance estimates of solitary ground nesting bee species: (A) *Agapostemon splendens*, (B) *Andrena miranda*, (C) *Lasioglossum acuminatum*, (D) *Lasioglossum coriaceum*, (E) *Lasioglossum leucozonium*, and (F) *Lasioglossum pilosum* in control, intermediate, mature and fresh sites across years (2007-2010) at Pinery and Turkey Point. Occupancy probabilities produced with PRESENCE software (Hines, 2006).

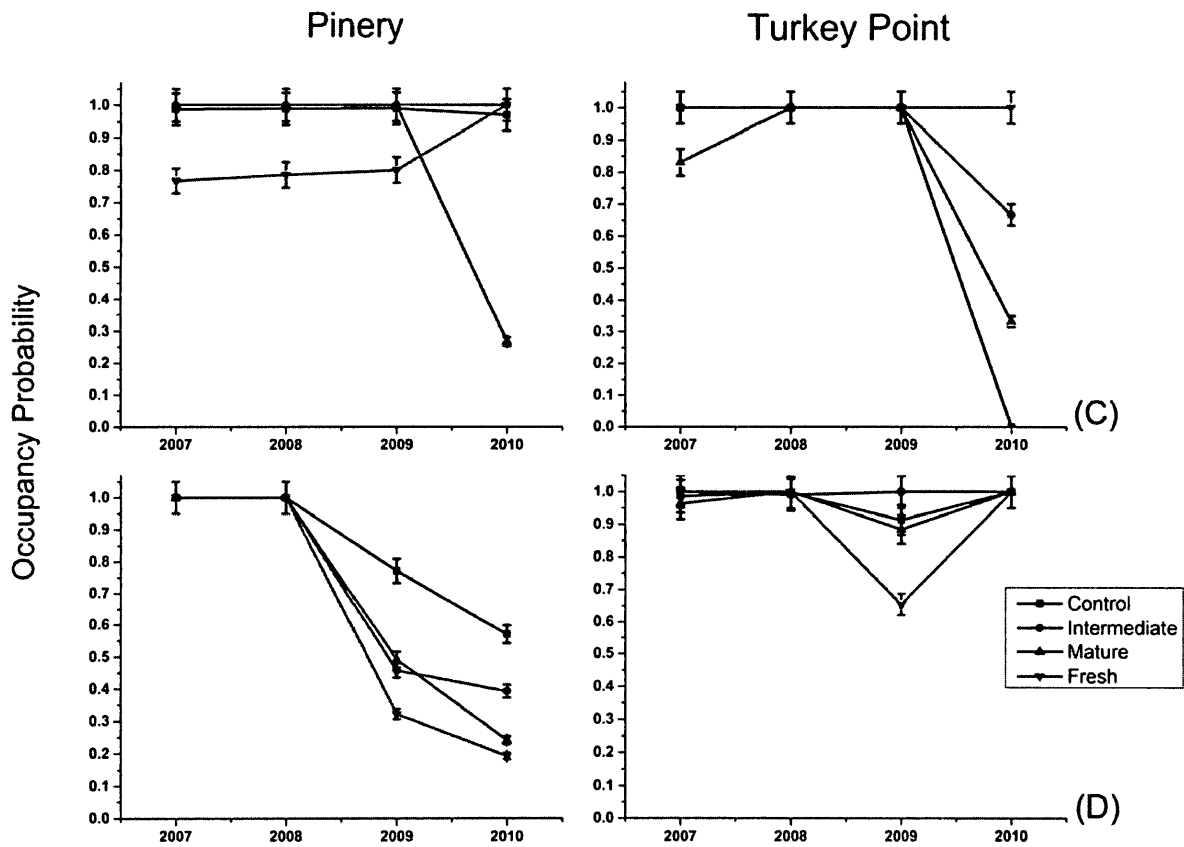


Figure 11 continued—Occupancy probabilities and variance estimates of solitary ground nesting bee species: (A) *Agapostemon splendens*, (B) *Andrena miranda*, (C) *Lasioglossum acuminatum*, (D) *Lasioglossum coriaceum*, (E) *Lasioglossum leucozonium*, and (F) *Lasioglossum pilosum* in control, intermediate, mature, and fresh sites across years (2007-2010) at Pinery and Turkey Point. Occupancy probabilities produced with PRESENCE software (Hines, 2006).

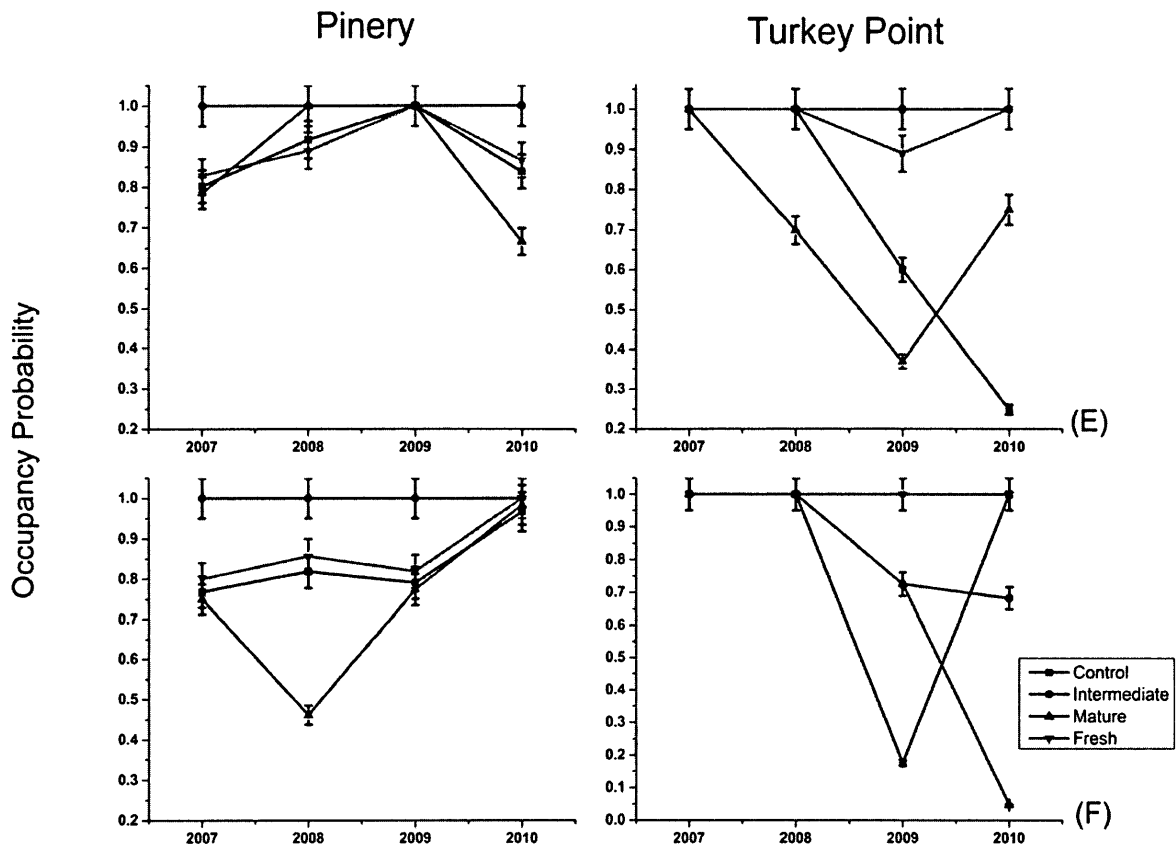


Figure 11 continued- Occupancy probabilities and variance estimates of solitary ground nesting bee species: (A) *Agapostemon splendens*, (B) *Andrena miranda*, (C) *Lasioglossum acuminatum*, (D) *Lasioglossum coriaceum*, (E) *Lasioglossum leucozonium*, and (F) *Lasioglossum pilosum* in control, intermediate, mature, and fresh sites across years (2007-2010) at Pinery and Turkey Point. Occupancy probabilities produced with PRESENCE software (Hines, 2006).

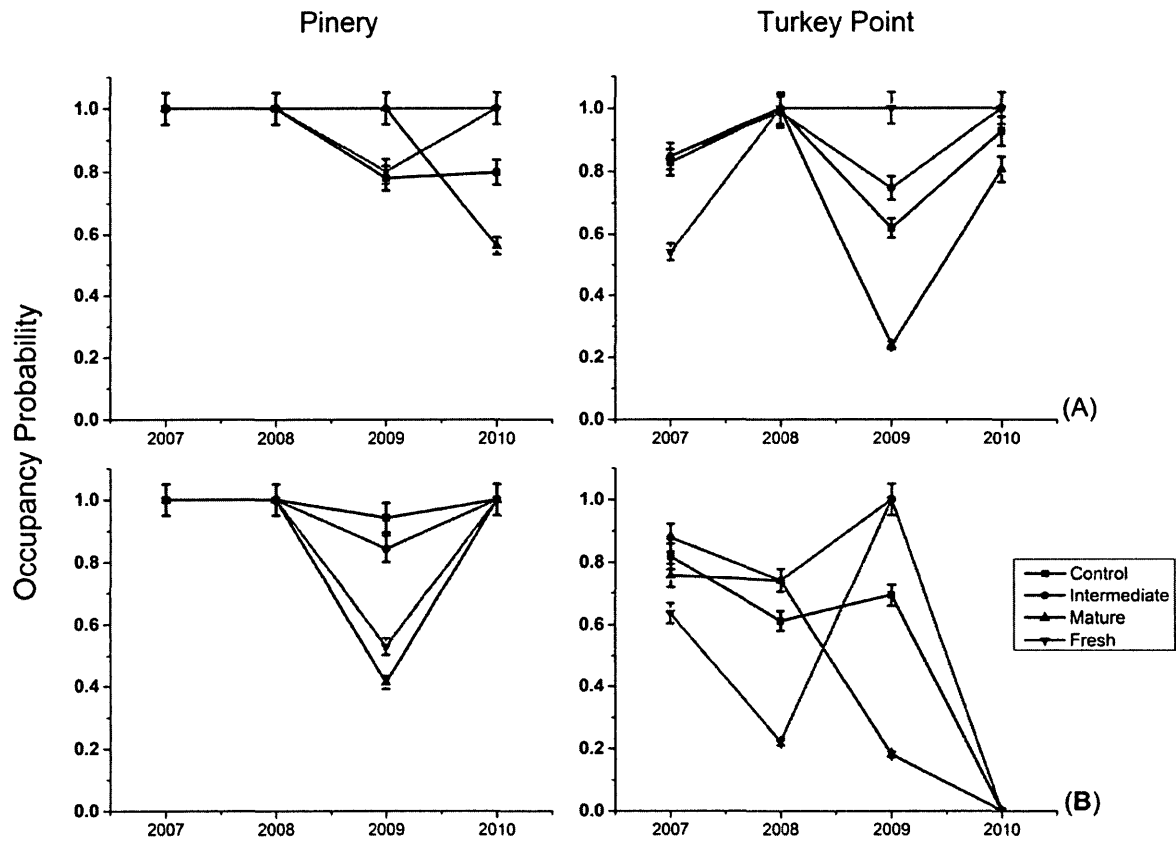


Figure 12- Occupancy probabilities and variance estimates of: (A) *Augochlorella aurata*, (B) *Bombus impatiens* in the *control*, *intermediate*, *mature* and *fresh* sites across years (2007-2010) at Pinery and Turkey Point. Occupancy probabilities produced with PRESENCE software (Hines, 2006).

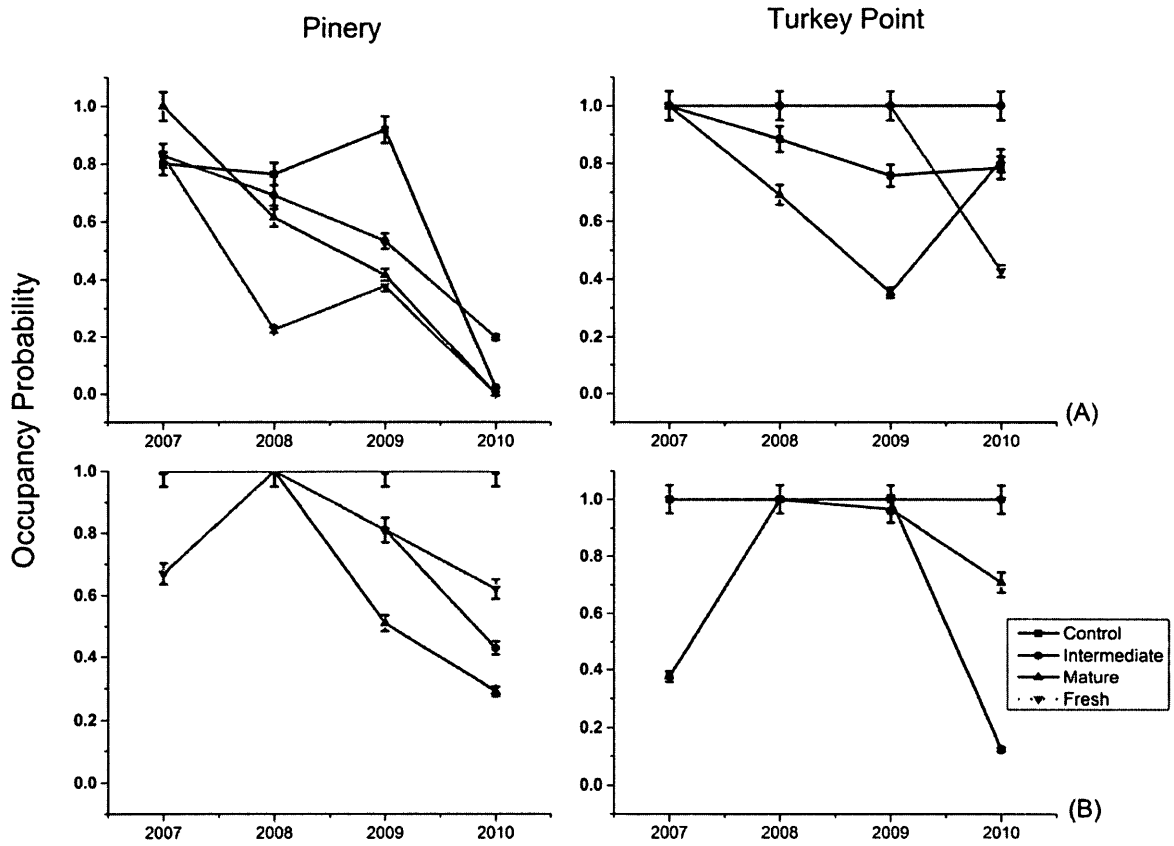


Figure 13- Occupancy probabilities and variance estimates of cavity nesters, (A) *Ceratina dupla* and (B) *Lasioglossum cressonii* in the *control*, *intermediate*, *mature* and *fresh* sites across years (2007-2010) at Pinery and Turkey Point. Occupancy probabilities produced with PRESENCE software (Hines, 2006).

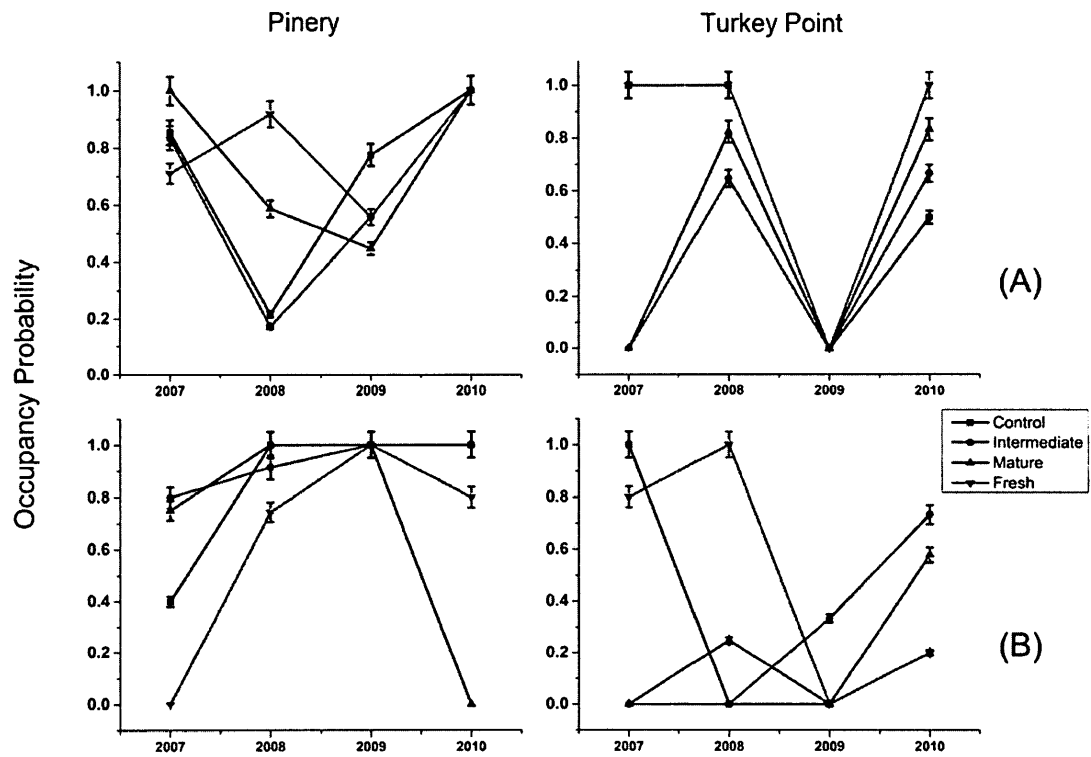


Figure 13- Occupancy probabilities and variance estimates of cleptoparasitic bee species: (A) *Nomada maculata* and (B) *Nomada sp.1* in the *control*, *intermediate*, *mature* and *fresh* sites across years (2007-2010) at Pinery and Turkey Point. Occupancy probabilities produced with PRESENCE software (Hines, 2006).

Table 7- Detection probabilities with 1 standard error for 12 bee species from Pinery.

Species	Survey 1	Survey 2	Survey 3	Survey 4	Survey 5	Survey 6	Survey 7	Survey 8	Survey 9	Survey 10
<i>Agapostemon splendens</i>										
2007	0.11[0]	-	0.59[0.12]	0.05[0.05]	0.32[0.11]	0.27[0.10]	0.53[0.12]	0.32[0.11]	0.05[0.05]	0.21[0.10]
2008	-	-	0.47[0.14]	-	-	0.20[0.11]	0.20[0.11]	0.61[0.15]	0.07[0.07]	0.50[0.5]
2009	0.12[0.08]	0.64[0.12]	0.76[0.11]	0.12[0.08]	0.52[0.12]	0.06[0.06]	0.12[0.08]	0.41[0.12]	0.29[0.11]	0.12[0.08]
2010	0.11[0.07]	0.47[0.11]	-	0.32[0.11]	0.11[0.07]	0.11[0.07]	0.50[0.23]	0.50[0.23]	0.50[0.23]	0.50[0.23]
<i>Andrena miranda</i>										
2007	0.18[0.09]	1.00[0]	-	0.06[0.06]	0.76[0.10]	-	-	-	-	0[0]
2008	0.80[0.10]	-	0.92[0.07]	-	-	-	-	-	-	0.50[0.23]
2009	0.71[0.11]	0.88[0.08]	0.94[0.06]	0.24[0.10]	-	0.71[0.11]	-	-	-	0[0]
2010	0.92[0.11]	0.85[0.10]	-	0.07[0.07]	-	0.57[0.13]	0.50[0.23]	0.50[0.23]	0.50[0.23]	0.50[0.23]
<i>Lasioglossum leucozonium</i>										
2007	0.24[0.11]	0.06[0.06]	0.30[0.11]	-	0.12[0.08]	0.06[0.06]	0.85[0.10]	0.43[0.12]	-	0.24[0.11]
2008	0.06[0.06]	-	0.61[0.17]	-	0.28[0.12]	-	0.06[0.06]	0.06[0.06]	0.06[0.06]	0.50[0.23]
2009	0[0.16]	0.42[0.11]	0.42[0.11]	0.21[0.09]	0.42[0.11]	0.05[0.05]	0.16[0.08]	0.05[0.05]	-	-
2010	0.55[0.13]	0.61[0.13]	0.06[0.06]	0.18[0.10]	0.31[0.12]	0.12[0.08]	0.50[0.23]	0.50[0.23]	0.50[0.23]	0.50[0.23]
<i>Lasioglossum acuminatum</i>										
2007	0.50[0.12]	0.34[0.11]	0.39[0.12]	0.06[0.05]	-	0.17[0.09]	0.28[0.11]	0.06[0.05]	0.56[0.12]	-
2008	0.56[0.12]	-	0.73[0.12]	-	0.06[0.05]	0.11[0.07]	0.17[0.09]	0.39[0.12]	-	0.50[0.23]
2009	0.72[0.11]	0.83[0.09]	0.89[0.07]	0.56[0.12]	0.06[0.05]	0.89[0.07]	0.06[0.05]	0.56[0.12]	0.50[0.12]	0.56[0.12]
2010	0.75[0.11]	0.68[0.12]	0.06[0.06]	0.93[0.06]	0.12[0.08]	-	0.50[0.23]	0.50[0.23]	0.50[0.23]	0.50[0.23]
<i>Lasioglossum coriaceum</i>										
2007	0.16[0.08]	0.21[0.09]	0.26[0.10]	-	0.05[0.23]	-	0.89[0.07]	0.89[0.07]	-	0.68[0.11]
2008	0.26[0.10]	0[0.21]	0.63[0.11]	0[0.21]	0.11[0.07]	0[0.21]	0.11[0.07]	0[0.21]	0[0.21]	0.50[0.23]
2009	0.20[0.16]	0.29[0.20]	-	-	0.20[0.16]	-	0.10[0.10]	-	-	-
2010	-	-	-	-	-	-	0.50	0.50	0.50	0.50
<i>Lasioglossum pilosum</i>										
2007	0.44[0.12]	-	1.00[0]	-	0.50[0.13]	0.06[0.06]	0.38[0.12]	0.31[0.12]	-	0.50[0.13]
2008	-	-	0.39[0.13]	-	0.52[0.14]	0.52[0.14]	0.06[0.06]	0.26[0.11]	0.06[0.06]	0.50[0.23]
2009	0.49[0.13]	0.18[0.10]	0.43[0.12]	0.55[0.12]	0.18[0.10]	0.31[0.11]	0.06[0.06]	0.18[0.10]	0.49[0.13]	0.25[0.11]
2010	0.21[0.10]	0.48[0.13]	0.21[0.10]	0.37[0.12]	0.27[0.11]	-	0.50[0.23]	0.50[0.23]	0.50[0.23]	0.50[0.23]

<i>Augochlorella aurata</i>										
2007	0.47[0.11]	0.68[0.11]	0.26[0.10]	0.05[0.05]	0.21[0.09]	0.47[0.11]	0.42[0.11]	0.84[0.08]	0.21[0.09]	-
2008							0.05[0.00]			
	0.26[0.10]	-	0.58[0.11]	0.05[0.05]	0.37[0.11]	0.37[0.11]	5]	0.37[0.11]	0.16[0.08]	0.50[0.23]
2009	0.47[0.12]	0.82[0.09]	0.76[0.10]	0.47[0.12]	0.29[0.11]	0.76[0.10]	0.29[0.11]	0.41[0.12]	0.53[0.12]	0.35[0.12]
2010	0.49[0.13]	0.67[0.12]	0.06[0.06]	0.67[0.12]	0.31[0.11]	0.37[0.12]	0.50[0.23]	0.50[0.23]	0.50[0.23]	0.50[0.23]
<i>Ceratina dupla</i>										
2007	0.73[0.11]	0.06[0.06]	0.24[0.11]	0.06[0.06]	-	-	0.55[0.13]	0.18[0.10]	-	0.61[0.12]
2008	0.44[0.18]	-	0.18[0.12]	-	0.09[0.09]	0.18[0.12]	-	0.35[0.16]	0.09[0.09]	0.50[0.23]
2009	0.36[0.16]	0.45[0.18]	0.27[0.14]	0.09[0.09]	0[0]	0.09[0.09]	-	-	0.09[0.09]	-
2010	0[0.08]	1.00[0]	0[0.08]	0.50[0.23]	0[0.08]	0[0.08]	0.50[0.23]	0.50[0.23]	0.50[0.23]	0.50[0.23]
<i>Lasioglossum cressonii</i>										
2007	0.17[0.09]	-	0.81[0.10]	0.06[0.06]	0.40[0.12]	0.63[0.12]	0.23[0.10]	0.12[0.08]	0.12[0.08]	-
2008	0.21[0.09]	-	0.58[0.11]	-	0.11[0.07]	-	0.05[0.05]	-	-	-
2009	0.40[0.13]	0.46[0.13]	0.40[0.13]	0.53[0.13]	0.07[0.06]	0.80[0.11]	-	0.40[0.13]	0.20[0.10]	0.27[0.11]
2010	0.52[0.15]	0.44[0.15]	0.09[0.08]	0.79[0.13]	0.26[0.13]	-	0.50[0.23]	0.50[0.23]	0.50[0.23]	0.50[0.23]
<i>Bombus impatiens</i>										
2007	-	-	-	0.05[0.05]	0.05[0.05]	-	-	-	-	-
2008	-	-	0.05[0.05]	-	0.05[0.05]	-	-	-	0.05[0.05]	0.50[0.23]
2009	0.07[0.07]	0.15[0.10]	-	0.07[0.07]	0.07[0.07]	0.15[0.10]	0.15[0.10]	0.44[0.15]	0.52[0.15]	0.15[0.10]
2010	0.05[0.05]	0[0.01]	0[0.01]	0.11[0.07]	0.16[0.08]	0.16[0.08]	0.50[0.23]	0.50[0.23]	0.50[0.23]	0.50[0.23]
<i>Nomada maculata</i>										
2007	0.12[0.10]	0[0.92]	0.35[0.21]	-	0.18[0.13]	0[0.92]	0[0.92]	0[0.92]	0[0.92]	0[0.92]
2008	0.14[0.14]	-	0.41[0.25]	-	0.27[0.20]	-	0.14[0.14]	-	-	0.50[0.23]
2009	0.60[0.35]	0.09[0.07]	0.09[0.07]	-	0.26[0.26]	0.09[0.07]	-	-	-	-
2010	0.05[0.05]	0.05[0.05]	-	-	-	-	0.50[0.23]	0.50[0.23]	0.50[0.23]	0.50[0.23]
<i>Nomada sp.1</i>										
2007	1	1	0.5[0.33]	-	-	-	0.42[0.2]	-	-	-
2008	-	1	0.33[0.27]	-	-	-	-	-	-	-
2009	-	1	-	0.5[0.33]	-	-	-	-	-	-
2010	0.5[0.35]	0.5[0.35]	-	-	-	0.60[0.1]	-	-	-	-

Table 8- Detection probabilities with 1 standard error for 12 bee species from Turkey Point Provincial Park.

Species Year	Survey 1	Survey 2	Survey 3	Survey 4	Survey 5	Survey 6	Survey 7
<i>Agapostemon splendens</i>							
2007	0[0.19]	0[0.19]	0[0.19]	0[0.19]	0.13[0.12]	0.38[0.17]	0[0.19]
2008	-	-	-	-	-	-	-
2009	0[0.9]	0.40[0.22]	0[0.10]	0[0.10]	0.2[0.18]	1[.33]	0[0.1]
2010	1[0]	-	-	-	-	0.5[0.23]	0.5[0.30]
<i>Andrena miranda</i>							
2007	0.50[0.35]	0[0.73]	1[0.19]	0[0.73]	0[0.73]	0[0.73]	0[0.73]
2008	0.12[.12]	0.75[.21]	0.25[.16]	0.25[.16]	-	-	-
2009	0.27[.17]	0.83[.15]	0.69[.18]	0.13[.13]	0[.67]	0[.67]	0.14[.13]
2010	-	0.52[0.24]	0.13[.13]	0.13[.13]	0.39[.21]	0.5[.30]	0.5[.30]
<i>Lasioglossum leucozonium</i>							
2007	0.13[0.12]	0.50[0.18]	0.38[0.17]	0.00[0.67]	0.13[0.12]	0.25[0.15]	0.38[0.17]
2008	0.42[0.19]	0.70[0.17]	0.70[0.17]	0.28[0.17]	0.00[0.74]	0.56[0.19]	0.14[0.13]
2009	0.40[0]	0.40[0]	0.40[0]	0.40[0]	0.40[0]	0.40[0]	0.40[0]
2010	0.31[0.19]	0.31[0.19]	0.31[0.19]	0.77[0.20]	0.00[0.0]	0.50[0.3]	0.50[0.30]
<i>Lasioglossum acuminatum</i>							
2007	0[.63]	0.13[0.15]	0.13[.15]	0[.45]	0.27[.22]	0.40[.30]	0.80[.49]
2008	0.75[0.15]	0.38[0.17]	0.50[0.18]	0[.63]	0[0.63]	0.25[0.15]	0.00[0.63]
2009	0.13[0.12]	0.38[0.17]	0.75[0.15]	0.50[0.18]	0.50[0.15]	0.13[0.12]	0.63[0.17]
2010	0.25[0.16]	1.00[0]	0.25[0.16]	-	0.25[0.16]	0.50[0]	0.50[0]
<i>Lasioglossum coriaceum</i>							
2007	0.13[0.12]	0.13[0.12]	0.25[0.16]	-	0.13[0.12]	0.38[0.18]	0.63[0.20]
2008	0.13[0.12]	0.50[0.20]	0.50[0.20]	0.25[0.16]	-	-	0.25[0.16]
2009	0.27[0.18]	0.27[0.18]	0.14[0.13]	0.14[0.13]	0.27[0.18]	0.27[0.18]	0.14[0.13]
2010	0.13[0.12]	0.13[0.12]	0[0.09]	0[0.09]	0.13[0.12]	0.50[0.03]	0.50[0.045]

Lasioglossum pilosum

2007	0.25[0.15]	0.25[0.15]	0.25[0.15]	0.13[0.12]	0.63[0.17]	0.50[0.18]	0.38[0.17]
2008	0.63[0.17]	0.13[0.12]	0.25[0.25]	0.38[0.17]	0.25[0.15]	0.88[0.12]	0.25[0.15]
2009	-	0.54[0.23]	-	0.54[0.23]	0.54[0.23]	-	-
2010	0.48[0.25]	0.48[0.25]	0.72[0.24]	0.24[0.21]	0.24[0.21]	0.50[0.18]	0.50[0.18]

Augochlorella aurata

2007	-	0.15[0.15]	0.15[0.15]	0.30[0.20]	0.30	0.30	-
2008	0.13[0.12]	0.75[0.21]	0.25[0.16]	0.25[0.16]	-	-	-
2009	0.20[0.19]	0.40[0.25]	0.20[0.19]	0.20[0.19]	-	0.20[0.19]	0.20[0.19]
2010	0.27[0.17]	0.13[0.13]	0.54[0.19]	0.67[0.19]	0.40[0.19]	0.50[0.18]	0.50[0.18]

<i>Ceratina dupla</i>								
2007	0.25[0.15]	0.13[0.12]	-	-	0.25[0.15]	0.63[0.17]	0.13[0.12]	
2008	0.42[0.19]	0.14[0.13]	0.42[0.19]	0.28[0.17]	0.42[0.19]	0.85[0.14]	0.42[0.19]	
2009	0.50[0.20]	0.50[0.20]	0.50[0.20]	0.33[0.19]	0.50[0.20]	0.66[0.19]	0.33[0.19]	
2010	0.16[0.15]	0.32[0.21]	-	0.32[0.21]	0.48[0.24]	0.50[0.18]	0.50[0.18]	
<i>Lasioglossum cressonii</i>								
2007	0.47[0.25]	0.47[0.25]	0.47[0.25]	0.23[0.21]	0.47[0.25]	-	-	
2008	0.13[0.12]	0.38[0.17]	0.13[0.12]	0.13[0.12]	-	-	-	
2009	0.38[0.18]	0.25[0.16]	0.13[0.12]	0.25[0.16]	0.13[0.12]	0.13[0.12]	0.51[0.21]	
2010	0.80[0.18]	0.80[0.18]	-	-	-	-	-	
<i>Bombus impatiens</i>								
2007	-	-	-	-	0.15[0.17]	0.15[0.17]	0.46[0.35]	
2008	-	-	-	-	0.41[0.26]	0.61[0.30]	0.20[0.19]	
2009	-	-	0.36[0.21]	0.36[0.21]	0.54[0.23]	0.18[0.17]	0.36[0.21]	
2010	-	-	-	-	-	-	-	
<i>Nomada maculata</i>								
2007	1[0.04]	0.50[0.35]	0.50[0.35]	-	-	-	-	
2008	0.16[0.15]	0.47[0.24]	0.16[0.15]	0.31[0.21]	-	0.16[0.15]	-	
2009	-	-	-	-	-	-	-	
2010	0.33[0.27]	0.50[0.35]	-	-	-	0.50[0.18]	0.50[0.18]	
<i>Nomada sp. 1</i>								
2007	1	1	0.5[0.33]	-	-	-	-	
2008	-	1	0.33[0.27]	-	-	-	-	
2009	-	1	-	0.5[0.33]	-	-	-	
2010	0.5[0.35]	0.5[0.35]	-	-	-	-	-	

5.0 Chapter 5- Summary of main findings and future work

5.1 Summary of main findings

Understanding how bees respond to environmental change is a crucial component to their conservation. This thesis demonstrates that fire disturbance plays a significant role in maintaining bee community diversity, composition, and how individual species occupy burned habitat in oak savannah remnants in Southern Ontario.

Reporting on the pre-disturbance bee community provided key insight into how bee communities and species are immediately affected by fire disturbance. Unlike published studies that investigated the impacts of fire on bee communities based on historical fire events, this work examined the impacts of fire on bee communities experimentally and is the first to do so.

Conventional alpha diversity metrics that are commonly used (species richness, species diversity and evenness) to test whether fire is an important disturbance for bee diversity showed bee diversity is highest shortly after fire events compared to many years post fire. My results agree with studies that have suggested fire to be an important disturbance for maintaining bee species diversity (Potts *et al.*, 2003; Noel *et al.*, 2006). But not all bee species are expected to respond similarly.

Assigning bee species to functional guilds based on nesting biology, body size etc. (Grixti and Packer, 2006; Williams *et al.*, 2010; Neame *et al.*, 2012; Sheffield *et al.*, 2013) may offer more insight into factors affecting bee community structure and community response to environmental disturbances (Sheffield *et al.*, 2013; Williams *et al.*, 2010). Here, I have shown that fire disturbance affects each guild differently. The

proportion of ground nesting species increased after fire whereas the proportion of cavity nesters decreased. A strong positive response from cleptoparasitic species to fire disturbance shows support for using rare species for indicator taxa of environmental disturbance (Sheffield *et al.*, 2013).

In chapter 4 I demonstrated that further refinement of community responses to fire can be obtained through the use of occupancy models. These revealed that bee species *within* guilds occupy burned habitat differently. Occupancy results strongly suggest that assigning bee species to functional guilds as currently understood may not depict true community level responses to environmental disturbances. A deeper understanding of the natural histories of each species is required.

5.2 Future work

Natural history information provides a crucial foundation for biodiversity studies (Dayton, 2003). Occupancy results presented above suggest the need for more work on ecologies of individual species. Therefore, more natural history information and attention to the fundamentals that help predict species response to environmental variation are warranted.

In this study, bee sampling took place over 4 consecutive years (2007-2010). It is recommended that more longer-term biodiversity studies be completed in different habitats to ensure a better understanding of species present within habitats.

Using functional guilds to determine community response to environmental disturbance is, without question, more effective than examining statistics based upon communities as a whole. It is recommended that future studies should not only continue to employ conventional functional guilds as recently used in the literature, but should also incorporate additional guilds. An additional guild should include specialist vs. generalist bee species. It is also recommended that studies using functional guilds explore combining guilds (e.g. small vs. large ground nesters) to determine community impacts. Perhaps dividing current guilds more finely- bare ground nesters, sparsely vegetated ground nesters, and densely vegetated ground nesters for example, would provide more insight into community structure and response.

Future work employing occupancy modeling is suggested to explore the variations in occupancy among species over decades and various environmental disturbances is warranted. Occupancy modeling completed in this thesis only examined bee species occupancy among single years and therefore could not investigate the effects of fire on colonization and extinction rates of bee species. Further investigation examining the probability that environmental disturbances such as fire effect the colonization and extinction of species within habitats is required.

5.3 References

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Appendix A

Table 9 - Complete list of species captured and identified from pan traps, at burn sites and control sites at Pinery Provincial Park and Turkey Point Provincial Park, Ontario, from 2007 to 2010.

Family and genus	subgenus and species	Sociality	Nesting habitat	2007		2008		2009		2010		Grand Total
				Pinery	Turkey	Pinery	Turkey	Pinery	Turkey	Pinery	Turkey	
Andrenidae												
<i>Andrena</i>	<i>algida</i>	Solitary	Ground	3		1		1	1	1	1	8
	<i>alleghehiensis</i>	Solitary	Ground	1	10	1		12	65	8	62	159
	<i>carlini</i>	Solitary	Ground								4	4
	<i>commoda</i>	Solitary	Ground	1								1
	<i>compacta</i>	Solitary	Ground		1							1
	<i>crataegi</i>	Solitary	Ground		1		10	1				12
	<i>distans</i>	Solitary	Ground	25	2							27
	<i>dunningi</i>	Solitary	Ground		1							1
	<i>fragariana</i>	Solitary	Ground	3	1							4
	<i>ilicis</i>	Solitary	Ground			2						2
	<i>imitatrix</i>	Solitary	Ground	3								3
	<i>lata</i>	Solitary	Ground		1							1
	<i>mendica</i>	Solitary	Ground	1		2	2					5
	<i>miranda</i>	Solitary	Ground	201	6	346	15	424	46	223	44	1304
	<i>miserabilis</i>	Solitary	Ground	3	1			3	3	1	6	17
	<i>nasonii</i>	Solitary	Ground	2	1			14				17
	<i>nothoscordi</i>	Solitary	Ground	2		4						6
	<i>obscuripennis</i>	Solitary	Ground		1							1
	<i>rubi</i>	Solitary	Ground				1	13				14

	<i>solidaginis</i>	Solitary	Ground	8	2							10
	<i>tridens</i>	Solitary	Ground	3								3
	<i>vicina</i>	Solitary	Ground	2		3	1					9 15
Apidae												
<i>Anthophora</i>	<i>terminalis</i>	Solitary	Stems									1 1
<i>Bombus</i>	<i>affinis</i>							1				1
	<i>ashtoni</i>					1						1
	<i>bimaculatus</i>	Eusocial	Undergro und	8	2	15	1	11		4		3 44
	<i>citrinus</i>	Parasitic	Host is B. impatiens	5		1						6
	<i>fervidus</i>	Eusocial	Ground surface						1	1		2
	<i>griseocollis</i>	Eusocial	Ground surface					1				1
	<i>impatiens</i>	Eusocial	Undergro und	2	8	4	6	31	8	9		68
	<i>mixtus</i>	Eusocial				1						1
	<i>perplexus</i>	Eusocial				2	1					3
	<i>rufocintus</i>	Eusocial	Undergro und				1					1
	<i>sandersoni</i>	Eusocial				1				1		2
	<i>vagans</i>	Eusocial		1	1			6	5			12
<i>Ceratina</i>	<i>calcarata</i>	Solitary	Stems	91	153	18	54	27	112	8		68 485
	<i>dupla</i>	Solitary	Stems	86	87	26	62	20	49	6		20 339
<i>Melissodes</i>	<i>desponsa</i>	Solitary	Ground			7						7
	<i>druriella</i>	Solitary	Ground	4	1		3	1	2			1 12
	<i>illata</i>	Solitary	Ground	1								1
<i>Nomada</i>	<i>articulata</i>	Parasitic	-		2	1	8		28			8 47
	<i>australis</i>	Parasitic	-		1		3					2 6
	<i>ceanothi</i>	Parasitic	-		14			6	48			68
	<i>cressonii</i>	Parasitic	-		12	5	28	5	48	6		20 124

<i>cuneata</i>	Parasitic	-	5	9							14
<i>denticulata</i>	Parasitic	-			2	2	9	37	1	1	52
<i>electella</i>	Parasitic	-	1	1							2
<i>fervida</i>	Parasitic	-					1				1
<i>festiva</i>	Parasitic	-		2							2
<i>florilega</i>	Parasitic	-		2							2
<i>graenicheri</i>	Parasitic	-					1	1			2
<i>illinoensis</i>	Parasitic	-		2	1		8	17	2	2	31
<i>lehighensis</i>	Parasitic	-	1	3							4
<i>lepida</i>	Parasitic	-					71	15			86
<i>louisianae</i>	Parasitic	-	2				38	41			81
<i>luteoloides</i>	Parasitic	-				1			1	1	3
<i>maculata</i>	Parasitic	-	18	11	5	8	23	10	2	7	84
<i>parva</i>	Parasitic	-		1							1
<i>perplexa</i>	Parasitic	-		2							2
<i>pseudops</i>	Parasitic	-	2	7							9
<i>pygmaea</i>	Parasitic	-	1	3	4	3	11	60	3	6	91
<i>sayi</i>	Parasitic	-	4	24	8	2	5	5			48
<i>sp.1</i>	Parasitic	-	51	6	142	4	5	1	116	6	329
<i>sp.10</i>	Parasitic	-			4		12	2			18
<i>sp.11</i>	Parasitic	-						1			1
<i>sp.2</i>	Parasitic	-	1	1	16	5	13	4	19	7	66
<i>sp.3</i>	Parasitic	-			12	5	2	4	11	7	41
<i>sp.4</i>	Parasitic	-	1					3			4
<i>sp.5</i>	Parasitic	-				1		1	8		10
<i>sp.6</i>	Parasitic	-	1	7				3		1	12
<i>sp.7</i>	Parasitic	-					3				3
<i>sp.8</i>	Parasitic	-					2	5			7

	<i>sp.9</i>	Parasitic	-						6		6
	<i>subnigrocincta</i>	Parasitic	-		1						1
Colletidae											
<i>Colletes</i>	<i>americanus</i>	Solitary	Ground					1	14		15
	<i>inaequalis</i>	Solitary	Ground					4	2	1	6 7
	<i>thoracica</i>	Solitary	Ground Stems/Ca vities			1					1
<i>Hylaeus</i>	<i>basalis</i>	Solitary	Stems Stems/Ca vities				2	1	1		2 6
	<i>illinoensis</i>	Solitary	Stems Stems/Ca vities	2	1						3
	<i>modestus</i>	Solitary							3		3 6
Halictidae											
<i>Agapostemon</i>	<i>sericeus</i>			4	16	12	40	7	57	1	14 151
	<i>splendens</i>			72	4	50		173	14	33	8 354
	<i>texana</i>					33	10	6		2	51
	<i>virescens</i>	Communal	Ground	1	51			1			53
<i>Augochlora</i>	<i>pura</i>	Solitary	Wood	28	9	11	2	13	15	3	2 82
<i>Augochlorella</i>	<i>aurata</i>	Eusocial Semisocial	Ground	132	10	163	8	310	13	131	22 789
<i>Augochloropsis</i>	<i>metallica</i>	?	Ground	1	3	6		1	2		13
<i>Halictus</i>	<i>confusus</i>	Solitary/Eu social	Ground	18	11	17	10	20	35	7	16 134
	<i>ligatus</i>	Solitary/Eu social	Ground	9		3	3	21	5	17	4 62
	<i>parallelus</i>	Solitary/Eu social	Ground		2	1	4				7
	<i>rubicundus</i> (<i>Dialictus</i>)			1			4	2	7		2 14
<i>Lasioglossum</i>	<i>abanci</i> (<i>Dialictus</i>) <i>admirandum</i>							8		3	11
	Eusocial?		Ground	4							4
	(<i>Dialictus</i>) <i>albipenne</i>	Eusocial?	Ground	1							1

<i>(Dialictus) anomalum</i>									1			1
<i>(Dialictus) atlanticum</i>			5	1	2							4
<i>(Dialictus) bruneri</i>			2	1	2	12	1	21			6	45
<i>(Dialictus) callidum</i>			1									1
<i>(Dialictus) caeruleum</i>	Eusocial	Wood	9	2	7	6	3	8	1		5	17
<i>(Dialictus) cressonii</i>	Eusocial?	Wood	81	29	97	8	151	20	59		17	462
<i>(Dialictus) divergens</i>	Solitary	Ground		5		1					3	9
<i>(Dialictus) ellisiae</i>	Eusocial?	Ground	2	4			1	7				14
<i>(Dialictus) ephialtum</i>	Eusocial?	Ground	8	2	5	1	4	1	1			22
<i>(Dialictus) foxii</i>	Solitary	Ground	1		1	2						4
<i>(Dialictus) laevissimum</i>	Eusocial	Ground	2									2
<i>(Dialictus) leucomum</i>	Eusocial?	Ground					25	41	87		91	244
<i>(Dialictus) lineatulum</i>	Eusocial?	Ground	3		1			4	1		1	10
<i>(Dialictus) lustrans</i>								1				1
<i>(Dialictus) mitchelli</i>	Eusocial	Ground					1					1
<i>(Dialictus) oblongum</i>	Eusocial	Ground	29	3	1							33
<i>(Dialictus) perihirtum</i>	Eusocial	Ground			1							1
<i>(Dialictus) perpunctatum</i>		Ground		1								1
<i>(Dialictus) pilosum</i>	Solitary	Ground	155	135	106	49	191	38	93		25	778

<i>(Dialictus) planatum</i>		Ground	2		18						20
<i>(Dialictus) rohweri</i>		Ground	13	1	1						15
<i>(Dialictus) sagax</i>		Ground		1							1
<i>(Dialictus) subviridatum</i>		Ground	27	2	20		13		10	4	76
<i>(Dialictus) taylorae</i>		Ground			3		16		6		19
<i>(Dialictus) tegulare</i>		Ground	1		1	2					4
<i>(Dialictus) timothyi</i>		Ground					91	15	19	6	126
<i>(Dialictus) versans</i>		Ground	1	2	2		2		2		9
<i>(Dialictus) versatum</i>		Ground					3	1	2		5
<i>(Dialictus) vierecki</i>	Solitary	Ground	8	32	5	26	1	20	6	13	111
<i>(Dialictus) zephyrum</i>		Ground	2	1	1						4
<i>(Dialictus) zophops</i>		Ground	38	2	61	24					126
<i>(Evyllaesus) cinctipes</i>	Eusocial	Ground	1								1
<i>(Evyllaesus) nelumbone</i>	Eusocial	Ground			1		1				2
<i>(Evyllaesus) pectoral</i>	Eusocial	Ground	13	5	7	11	29	7	12	7	88
<i>(Lasioglossum) acuminatum</i>	Solitary	Ground	82	24	353	25	676	82	229	13	1391
<i>(Lasioglossum) coriaceum</i>	Solitary	Ground	393	56	44	22	10	16	1	5	543
<i>(Lasioglossum) forbesii</i>	Solitary	Ground					1	2	3	2	8
<i>(Lasioglossum) fuscipenne</i>	Solitary	Ground	4	4	11	5	2	4	1	3	33

	<i>(Lasioglossum) leucozonium</i>		Ground	62	29	70	34	78	62	47	22	393
	Solitary											
	<i>(Lasioglossum) paraforbesii</i>		Ground				1	7				
	<i>(Lasioglossum) zonulum</i>		Ground	3	1	4	2	1				11
<i>Sphcodes</i>	<i>aroniae</i>	Parasitic	-					3	2			5
	<i>atlantis</i>	Parasitic	-		1			5	3			9
	<i>banksii</i>	Parasitic	-		1	1					1	3
	<i>confertus</i>	Parasitic	-	2	2	8	7	2			1	22
	<i>davisii</i>	Parasitic	-		46							46
	<i>dichrous</i>	Parasitic	-	4	13			2	34	9	8	70
	<i>galerus</i>	Parasitic	-						1			1
	<i>illinoensis</i>	Parasitic	-		1							1
	<i>persimilis</i>	Parasitic	-			2	1		2	2	11	5
	<i>phosphorus</i>	Parasitic	-			1	1	2	3			1
	<i>prostygus</i>	Parasitic	-			7	4		3	6	2	22
	<i>ranunculi</i>	Parasitic	-	4	2	10	10	23	8	2	1	60
	<i>solonis</i>	Parasitic	-		6				1	1	3	11
	<i>stygius</i>	Parasitic	-	5	3	4		2				14
Megachilidae												
<i>Anthidium</i>	<i>manicatum</i>	Solitary	Cavities	2								2
<i>Coelioxys</i>	<i>octodentata</i>	Parasitic	-								2	2
	<i>rufitarsis</i>	Parasitic	-	5	6							10
	<i>sodalis</i>	Parasitic	-						1			1
<i>Hoplitis</i>	<i>pilosifrons</i>	Solitary	Cavities	2	1		14		3			19
	<i>spoliata</i>	Solitary	Cavities	1		2	1					4
	<i>truncata</i>	Solitary	Cavities	1					4			5
<i>Megachile</i>	<i>addenda</i>	Solitary					8			1	4	13
	<i>apicalis</i>	Solitary	Cavities	1								1

	<i>brevis</i>	Solitary	Cavities	1		3	2				6
	<i>dentitarsus</i>	Solitary	Cavities					1	6		7
	<i>gemula</i>	Solitary	Cavities	1		5		2	2	1	2 13
	<i>latimanus</i>	Solitary	Ground	2	2	1				2	2 9
	<i>melanophoea</i>	Solitary	Ground Cavities/G				2		1		3
	<i>mendica</i>	Solitary	round	6	5	1			5		17
	<i>perihirta</i>	Solitary	Cavities	3							3
	<i>pugnata</i>	Solitary	Cavities		1						1
	<i>relativa</i>	Solitary	Cavities	7	5	3		2			17
	<i>texana</i>	Solitary	Ground				3		4		7
<i>Osmia</i>	<i>albiventris</i>	Solitary	Cavities	1		1		1			2 5
	<i>atriventris</i>	Solitary	Cavities	43	8	91	4	57	5	7	4 219
	<i>bucephala</i>	Solitary	Cavities	20	1	45		25		27	118
	<i>caerulescens</i>	Solitary	Cavities	1	1	1					3
	<i>collinsiae</i>	Solitary	Cavities Snail			14		2		2	18
	<i>conjuncta</i>	Solitary	shells	9		9		1		2	21
	<i>cordata</i>	Solitary	Cavities			1					1
	<i>distincta</i>	Solitary	Cavities	9	4						13
	<i>felti</i>	Solitary	Cavities	8		9		12	1		30
	<i>georgica</i>	Solitary	Cavities	5	3	51	2	39	20	13	7 140
	<i>illinoensis</i>	Solitary	Cavities	2	3						5
	<i>lignaria</i>	Solitary	Cavities	1							1 2
	<i>michiganensis</i>	Solitary	Cavities			11		7	2	1	21
	<i>proxima</i>	Solitary	Cavities			2	1				1 4
	<i>pumila</i>	Solitary	Cavities			41		16	17		74
	<i>sandhousae</i>	Solitary	Cavities	1							1
	<i>simillima</i>	Solitary	Cavities			3	1	1	1		6

Family and genus	subgenus and species	Sociality	Nesting habitat									Grand Total
				2007		2008		2009		2010		
				Pinery	Turkey	Pinery	Turkey	Pinery	Turkey	Pinery	Turkey	
	<i>sp. c</i>	Solitary	Cavities	14		91	1	68	5	50	7	236
	<i>subfasciata</i>	Solitary	Cavities						2			2
	<i>texana</i>	Solitary	Cavities	1		1						2
												116
				1934	957	2179	615	2911	1287	1335	649	10

Appendix B

The following from Turkey Point control site in 2007 demonstrates how lognormal plots were constructed for each site/year and locality following Magurran (2004). Guild association for each species is also found.

	Gu	P2	Log2	x-xbar
	ild			
<i>Ceratina dupla</i>	C	29	4.857980995	2.885390995
<i>Agapostemon virescens</i>	A	21	4.392317423	2.419727423
<i>Ceratina calcarata</i>	C	19	4.247927513	2.275337513
<i>Lasioglossum pilosum</i>	A	19	4.247927513	2.275337513
<i>Lasioglossum cressonii</i>	C	17	4.087462841	2.114872841
<i>Lasioglossum vierecki</i>	A	15	3.906890596	1.934300596
<i>Nomada sayi</i>	D	13	3.700439718	1.727849718
<i>Lasioglossum leucozonium</i>	A	12	3.584962501	1.612372501
<i>Andrena allegheniensis</i>	A	9	3.169925001	1.197335001
<i>Agapostemon sericeus</i>	A	8	3	1.02741
<i>Lasioglossum coriaceum</i>	A	8	3	1.02741
<i>Halictus confusus</i>	B	6	2.584962501	0.612372501
<i>Nomada cuneata</i>	D	6	2.584962501	0.612372501
<i>Lasioglossum acuminatum</i>	A	5	2.321928095	0.349338095
<i>Lasioglossum divergens</i>	A	5	2.321928095	0.349338095
<i>Nomada ceanothi</i>	D	5	2.321928095	0.349338095
<i>Nomada cressonii</i>	D	5	2.321928095	0.349338095
<i>Nomada sp.1</i>	D	4	2	0.02741
<i>Osmia atriventris</i>	C	4	2	0.02741
<i>Sphecodes davisii</i>	D	4	2	0.02741
<i>Sphecodes solonis</i>	D	4	2	0.02741
<i>Augochlora pura</i>	B	3	1.584962501	-0.387627499
<i>Augochlorella aurata</i>	B	3	1.584962501	-0.387627499
<i>Nomada maculata</i>	D	3	1.584962501	-0.387627499
<i>Nomada pseudops</i>	D	3	1.584962501	-0.387627499
<i>Peponapis pruinosa</i>	A	3	1.584962501	-0.387627499
<i>Agapostemon splendens</i>	A	2	1	-0.97259
<i>Andrena distans</i>	A	2	1	-0.97259
<i>Andrena miranda</i>	A	2	1	-0.97259
<i>Andrena solidaginis</i>	A	2	1	-0.97259
<i>Bombus impatiens</i>	E	2	1	-0.97259
<i>Halictus parallelus</i>	B	2	1	-0.97259
<i>Lasioglossum ellisiae</i>	A	2	1	-0.97259

<i>Lasioglossum pectoralis</i>	A	2	1	-0.97259
<i>Megachile latimanus</i>	A	2	1	-0.97259
<i>Nomada florilega</i>	D	2	1	-0.97259
<i>Nomada pygmaea</i>	D	2	1	-0.97259
<i>Osmia distincta</i>	C	2	1	-0.97259
<i>Andrena fragariana</i>	A	1	0	-1.97259
<i>Andrena nasonii</i>	A	1	0	-1.97259
<i>Andrena obscurpennis</i>	A	1	0	-1.97259
<i>augochloropis metallica</i>	B	1	0	-1.97259
<i>Ceolioxys rufitarsis</i>	D	1	0	-1.97259
<i>Hoplitis pilosifrons</i>	C	1	0	-1.97259
<i>Lasioglossum ephialtum</i>	A	1	0	-1.97259
<i>Lasioglossum fuscipenne</i>	A	1	0	-1.97259
<i>Lasioglossum oblongum</i>	A	1	0	-1.97259
<i>Lasioglossum paraforbesii</i>	A	1	0	-1.97259
<i>Lasioglossum perpunctatum</i>	A	1	0	-1.97259
<i>Lasioglossum sagax</i>	A	1	0	-1.97259
<i>Lasioglossum subviridatum</i>	A	1	0	-1.97259
<i>Lasioglossum versans</i>	A	1	0	-1.97259
<i>Lasioglossum versatum</i>	A	1	0	-1.97259
<i>Lasioglossum zephyrum</i>	A	1	0	-1.97259
<i>Megachile mendica</i>	C	1	0	-1.97259
<i>Megachile relativa</i>	C	1	0	-1.97259
<i>Melissodes druriella</i>	A	1	0	-1.97259
<i>Nomada articulata</i>	D	1	0	-1.97259
<i>Nomada electella</i>	D	1	0	-1.97259
<i>Nomada illinoense</i>	D	1	0	-1.97259
<i>Nomada lehighensis</i>	D	1	0	-1.97259
<i>Nomada perplexa</i>	D	1	0	-1.97259
<i>Nomada sp.2</i>	D	1	0	-1.97259
<i>Osmia bucephala</i>	C	1	0	-1.97259
<i>Osmia illinoensis</i>	C	1	0	-1.97259
<i>Sphecodes atlantis</i>	D	1	0	-1.97259
<i>Sphecodes confertus</i>	D	1	0	-1.97259
<i>Sphecodes dichrous</i>	D	1	0	-1.97259

Total Individ	289	for Xo	log10(0.5)	log2(0.5)						
			0.3010299							
Total species	69	0.5	96	-1						
mean log2	1.240264985									
Var log2	2.937938833									
(mean-Xo)	5.018787204		a	b	c	d	e	f	g	h
y	0.585388205	1	0.5	-1	0.590975459	26.47113074		0	-0.5	
O	0.4103	2	1.5	0.584962501	0.118043616	52.22112852	28.13035852	22	21.5	-6.630358521
mean-Xo	2.240264985	3	2.5	1.321928095	0.447718711	64.23506683	40.14429683	33	32.5	-7.644296826
	2.235429986	4	4.5	2.169925001	0.827062691	75.98539995	51.89462995	42	41.5	-10.39462995
Ux	0.321084262	5	8.5	3.087462841	1.237515197	85.16521904	61.07444904	49	48.5	-12.57444904
Vx	4.997147223	6	16.5	4.044394119	1.665590012	90.89829739	66.80752739	55	54.5	-12.30752739
Zo	0.590975459	7	32.5	5.022367813	2.103077967	93.7784775	69.6877075	58	57.5	-12.1877075
Po	0.277268432	8	64.5	6.011227255	2.545435567	94.9501376	70.8593676	60	59.5	-11.3593676
		9	128.5	7.005624549	2.990270475	95.33807715	71.24730715	63	62.5	-8.747307153
S*	95.47113074	10	256.5	8.002815016	3.436354885	95.44298594	71.35221594	65	64.5	-6.852215942
D	0.488338199									
P(0.01)	0.1067155									
P(0.05)	0.091287086									

Appendix C

Table 10- Multiple comparison test of proportions from Pinery, fresh Site using the modified Freeman and Tukey transformation (Zar, 1999).

GUILD A	2007 619/1013=0.61 a	2008 136/200=0.68 ab	2009 675/1012=0.67 b	2010 240/377= 0.47 c
Comparison	Difference	SE	q	q
2008 vs 2010	55.55-43.4= 12.15	1.77	6.86	3.63
2008 vs 2007	55.55-51.42= 4.13	1.57	2.63	3.63
2009 vs 2007	54.75-51.42= 3.33	0.897	3.71	3.63
2007 vs 2010	51.42-43.4= 8.02	1.22	6.57	3.63
GUILD B	2007 116/1013=0.11 a	2008 15/200=0.07 a	2009 117/1012=0.17 b	2010 73/377= 0.19 c
Comparison	Difference	SE	q	q
2010 vs 2008	26.11-15.89=10.22	1.77	5.77	3.63
2010 vs 2007	26.11-19.78=6.33	1.22	5.19	3.63
2009 vs 2007	24.49-19.78=4.71	0.897	5.25	3.63
2009 vs 2008	24.49-15.89=8.6	1.57	5.48	3.63
2007 vs 2008	26.11-24.49=1.62	1.57	1.03	3.63
GUILD C	2007 116/1013=0.11 a	2008 23/200=0.12 a	2009 15/1012=0.09 b	2010 22/377= 0.64 c
Comparison	Difference	SE	q	q
2010 vs 2009	52.93-17.34=35.59	0.9	39.5	3.63
2010 vs 2008	52.93-19.82=33.11	1.77	18.71	3.63
2010 vs 2007	52.93-27.98=24.95	1.22	20.45	3.63
2007 vs 2009	27.98-17.34=10.64	0.897	11.86	3.63
2007 vs 2008	27.98-19.82=8.16	1.57	5.19	3.63
GUILD D	2007 47/1013=0.0.5 a	2008 22/200=0.11 b	2009 66/1012=0.06 a	2010 22/377= 0.19 c
Comparison	Difference	SE	q	q
2009 vs 2008	19.37-14.05=5.32	1.57	3.38	3.63
2010 vs 2009	26.1-19.37=6.73	0.9	7.47	3.63
2008 vs 2007	14.05-12.437=1.61	11.57	1.02	3.63
GUILD E	2007 8/1013=0.008 a	2008 4/200=0.02 b	2009 8/1012=0.008 a	2010 6/377= 0.06 c
Comparison	Difference	SE	q	q
2010 vs 2008	13.979-8.13=5.85	1.77	3.30	3.63
2008 vs 2009	8.13-5.101=3.02	1.57	1.92	3.63
2010 vs 2009	13.979-5.101=8.87	0.9	9.86	3.63

Table 11- Multiple comparison test of proportions from Pinery, intermediate site using the modified Freeman and Tukey transformation (Zar, 1999).

GUILD A	2007 727/1019=0.71 a	2008 489/883=0.55 a	2009 782/1468=0.53 b	2010 546/1019= 0.71 b
Comparison	Difference	SE	q	q
2007 vs 2009	57.6-46.87=10.73	0.826	12.98	3.63
2007 vs 2008	57.6-48.09=9.51	0.931	10.21	3.63
GUILD B	2007 72/1019=0.075 a	2008 64/883=0.072 a	2009 97/1468=0.066 a	2010 14/770= 0.018 b
Comparison	Difference	SE	q	q
2007 vs 2010	15.84-7.74=8.1	0.967	8.37	3.63
2007 vs 2009	15.84-14.89=0.95	0.826	1.14	3.63
2008 vs 2009	15.62-14.89=0.73	0.863	0.846	3.63
GUILD C	2007 138/1019=0.14 a	2008 234/883=0.27 ac	2009 261/1468=0.18 abc	2010 119/770= 0.15 b
Comparison	Difference	SE	q	q
2008 vs 2007	30.98-21.59=9.39	0.931	10.08	3.63
2008 vs 2010	30.98-23.15=7.83	0.998	7.84	3.63
2008 vs 2009	30.98-24.94=6.04	0.863	7.00	3.63
2009 vs 2007	24.94-21.59=3.35	0.826	4.05	3.63
2009 vs 2010	24.94-23.15=1.79	0.901	1.99	3.63
GUILD D	2007 57/1019=0.056 a	2008 85/883=0.096 b	2009 261/1468=0.18 c	2010 84/770= 0.109 b
Comparison	Difference	SE	q	Q
2009 vs 2007	26.92-13.68=13.24	0.825	16.05	3.63
2009 vs 2008	26.92-18.07=8.85	0.863	10.26	3.63
2009 vs 2010	26.92-19.28=7.64	0.901	8.47	3.63
2008 vs 2007	18.07-13.68=4.39	0.931	4.71	3.63
2010 vs 2008	19.28-18.07=1.21	0.998	1.211	3.63
GUILD E	2007 21/1019=0.021 a	2008 11/883=0.012 a	2009 27/1468=0.018 a	2010 7/770= 0.009 a
Comparison	Difference	SE	q	Q
2007 vs 2010	8.17-5.47=2.7	0.967	2.79	3.63
2007 vs 2008	8.17-6.42=1.75	0.931	1.88	3.63
2007 vs 2009	8.17-7.8=0.37	0.826	0.45	3.63
2009 vs 2008	7.8-6.42=1.38	0.863	1.60	3.63

Table 12- Multiple comparison test of proportions from Pinery, mature site using the modified Freeman and Tukey transformation (Zar, 1999).

GUILD A	2007 257/573=0.45 a	2008 421/786=0.54 b	2009 123/307=0.40 ac	2010 105/178= 0.59 bd
Comparison	Difference	SE	q	q
2010 vs 2009	50.178-39.23=10.9	1.91	5.71	3.63
2010 vs 2007	50.178-42.04=8.14	1.74	4.68	3.63
2010 vs 2008	50.178-47.04=3.14	1.68	1.87	3.63
2008 vs 2007	47.04-42.04=5	1.1	4.5	3.63
2007 vs 2009	42.04-39.23=2.81	1.43	1.96	3.63
2008 vs 2009	47.04-39.23=7.81	1.36	5.74	3.63
GUILD B	2007 23/573=0.04 a	2008 47/786=0.06 a	2009 39/307=0.13 b	2010 26/178= 0.15 b
Comparison	Difference	SE	q	q
2010 vs 2007	22.47-11.55=10.92	1.74	6.28	3.63
2010 vs 2008	22.47-14.15=8.32	1.68	4.95	3.63
2009 vs 2008	20.88-14.15=6.73	1.36	4.95	3.63
2010 vs 2009	22.47-20.88=1.59	1.91	0.83	3.63
GUILD C	2007 224/573=0.39 a	2008 207/786=0.26 b	2009 47/307=0.15 ac	2010 27/178= 0.15 c
Comparison	Difference	SE	q	q
2007 vs 2010	38.7-22.91=15.79	1.74	9.07	3.63
2007 vs 2009	38.7-23.03=15.67	1.43	10.95	3.63
2007 vs 2008	38.7-30.87=7.83	1.11	7.05	3.63
2008 vs 2009	30.87-23.03=7.84	1.36	5.76	3.63
GUILD D	2007 57/573=0.099 a	2008 105/786=0.10 a	2009 97/307=0.32 b	2010 18/178= 0.10 a
Comparison	Difference	SE	q	q
2009 vs 2007	34.2-18.38= 15.82	1.43	11.06	3.63
2009 vs 2010	34.2-18.54=15.66	1.91	8.20	3.63
2009 vs 2008	34.2-21.44=12.76	1.36	9.38	3.63
2008 vs 2007	21.44-18.54=2.9	1.11	2.61	3.63
GUILD E	2007 12/573=0.021 a	2008 6/786=0.007 a	2009 1/307=0.003 a	2010 5/178= 0.011 a
Comparison	Difference	SE	q	q
2007 vs 2009	8.31-3.27= 5.04	1.43	3.52	3.63
2007 vs 2008	8.31-5.01= 3.3	1.11	2.97	3.63
2007 vs 2010	8.31-6.084=2.26	1.74	1.30	3.63

Table 13- Multiple comparison test of proportions from Pinery, control site using the modified Freeman and Tukey transformation (Zar, 1999).

GUILD A	2007 546/1127=0.48 a	2008 406/829=0.49 a	2009 726/1251=0.58 b	2010 213/495= 0.43 a
Comparison	Difference	SE	q	q
2007 vs 2009	49.6-43.85=5.75	0.832	6.91	3.63
2010 vs 2009	49.6-40.99=8.61	1.075	8.003	3.63
2009 vs 2008	44.4-40.9=3.5	0.9070	5.733	3.63
GUILD B	2007 50/1127=0.04 a	2008 29/829=0.035 a	2009 67/1251=0.054 a	2010 29/495= 0.053 a
Comparison	Difference	SE	q	q
2009 vs 2008	13.32-10.78=2.54	0.9070	2.8	3.63
2009 vs 2007	13.32-11.54=1.78	0.832	2.14	3.63
GUILD C	2007 403/1127=0.36 a	2008 250/829=0.30 b	2009 269/1251=0.22 c	2010 121/495= 0.22 a
Comparison	Difference	SE	q	q
2007 vs 2009	36.87-27.97=8.9	0.832	10.7	3.63
2007 vs 2010	36.87-28.08=8.79	1.092	8.051	3.63
2007 vs 2008	36.87-33.21=3.66	0.927	3.95	3.63
2008 vs 2010	33.21-28.08=5.13	1.15	4.46	3.63
GUILD D	2007 117/1127=0.1 a	2008 135/829=0.16 b	2009 165/1251=0.32 a	2010 129/495= 0.24 c
Comparison	Difference	SE	q	q
2010 vs 2007	29.08-18.43= 10.65	1.092	9.755	3.63
2010 vs 2009	29.08-21.3= 7.78	1.075	7.23	3.63
2010 vs 2008	29.08-23.58=5.5	1.15	4.78	3.63
2009 vs 2007	21.3-18.43= 2.87	0.832	3.45	3.63
2008 vs 2009	23.58-21.3= 2.28	0.9070	2.51	3.63
GUILD E	2007 11/1127=0.009 a	2008 9/829=0.011 a	2009 24/1251=0.019 a	2010 3/495= 0.055 a
Comparison	Difference	SE	q	q
2009 vs 2010	7.92-4.25=3.67	1.075	3.413	3.63
2009 vs 2007	7.92-5.44=2.48	0.8317	2.98	3.63
2009 vs 2008	7.92-6.02=2.98	0.9070	3.29	3.63

Table 14- Multiple comparison test of proportions from Turkey Point, fresh site using the modified Freeman and Tukey transformation (Zar, 1999).

GUILD A	2007 90/149=0.60 a	2008 13/26= 0.50 a	2009 85/126=0.67 a	2010 26/40=0.65 a
Comparison	Difference	SE	q	q
2009 vs 2008	54.94-45=9.94	4.3	2.931	3.63
GUILD B	2007 15/149=0.10 a	2008 2/26= 0.077 a	2009 17/126=0.13 a	2010 3/40= 0.075 a
Comparison	Difference	SE	q	q
2009 vs 2008	21.1-16.11=4.99	4.3	1.16	3.63
GUILD C	2007 24/149=0.16 a	2008 9/26=0.35 a	2009 16/126=0.13 a	2010 4/40= 0.10 a
Comparison	Difference	SE	q	q
2008 vs 2007	36.27- 23.58=12.59	4.27	2.95	3.63
GUILD D	2007 19/149=0.13 a	2008 2/26=0.16 a	2009 8/126=0.06 a	2010 6/40= 0.15 a
Comparison	Difference	SE	q	q
2010 vs 2009	22.79-14.18=8.61	3.66	2.35	3.63
GUILD E	2007 1/149=0.007 a	2008 0 b	2009 0 b	2010 1/40=0.025 a
Comparison	Difference	SE	q	q
2010 vs 2007	9.10-4.799=4.301	2.45	1.76	3.63

Table 15- Multiple comparison test of proportions from Turkey Point, intermediate site using the modified Freeman and Tukey transformation (Zar, 1999).

GUILD A	2007 143/262=0.55 a	2008 164/315= 0.52 a	2009 336/835=0.40 b	2010 220/397=0.55 a
Comparison	Difference	SE	q	q
2007 vs 2009	47.87-39.23= 8.64	1.43	6.04	3.63
2008 vs 2009	46.15-39.23=6.92	1.39	4.98	3.63
2010 vs 2008	47.86-46.15=1.71	1.53	1.11	3.63
GUILD B	2007 11/262=0.042 a	2008 12/315= 0.038 a	2009 32/835=0.038 a	2010 28/397= 0.071 a
Comparison	Difference	SE	q	q
2010 vs 2008	15.45-11.8=3.65	1.53	2.38	3.63
GUILD C	2007 58/262=0.22 a	2008 89/315=0.28 a	2009 182/835=0.22 a	2010 86/397= 0.28 a
Comparison	Difference	SE	Q	q
2008 vs 2007	31.95-27.97=3.98	1.69	2.36	3.63
GUILD D	2007 44/262=0.17 a	2008 44/315=0.14 a	2009 277/835=0.33 b	2010 61/397= 0.15 a
Comparison	Difference	SE	q	q
2009 vs 2007	35.06- 24.35=10.71	1.43	7.49	3.63
GUILD E	2007 6/262=0.023 a	2008 6/315=0.019 a	2009 8/835=0.01 a	2010 2/397=0.005 a
Comparison	Difference	SE	q	q
2007 vs 2010	8.72-4.05=4.67	1.61	2.90	3.63

Table 16- Multiple comparison test of proportions from Turkey Point, mature site using the modified Freeman and Tukey transformation (Zar, 1999).

GUILD A	2007 37/95=0.39 a	2008 108/199= 0.54 b	2009 52/164=0.32 a	2010 55/100=0.55 b
Comparison	Difference	SE	q	q
2008 vs 2007	47.29-38.6=8.69	2.26	3.84	3.63
GUILD B	2007 9/95=0.095 a	2008 13/199= 0.065 a	2009 7/164=0.043 a	2010 3/100= 0.03 a
Comparison	Difference	SE	q	q
2007 vs 2010	17.95-9.97=7.98	2.89	2.76	3.63
GUILD C	2007 28/95=0.29 a	2008 39/199=0.20 a	2009 27/164=0.16 a	2010 24/100= 0.24 a
Comparison	Difference	SE	Q	q
2007 vs 2009	32.58-23.5=9.08	2.61	3.48	3.63
GUILD D	2007 19/95=0.20 a	2008 36/199=0.18 a	2009 77/164=0.47 b	2010 18/100= 0.18 a
Comparison	Difference	SE	q	q
2009 vs 2008	43.28- 25.1=18.18	2.13	8.53	3.63
GUILD E	2007 2/95=0.021 a	2008 3/199=0.015 a	2009 1/164=0.006 a	2010 0 a
Comparison	Difference	SE	q	q
2007 vs 2009	8.33-4.44=3.89	2.61	1.49	3.63
2007 vs 2010	8.33-0=8.33	2.89	2.88	3.63

Table 17- Multiple comparison test of proportions from Turkey Point, control site using the modified Freeman and Tukey transformation (Zar, 1999).

GUILD A	2007 135/288=0.47 a	2008 41/67= 0.61 a	2009 49/102=0.48 a	2010 8/16=0.50 a
Comparison	Difference	SE	q	q
2008 vs 2007	51.35-43.28=8.07	2.74	2.92	3.63
GUILD B	2007 15/288=0.05 a	2008 1/67= 0.15 a	2009 6/102=0.06 a	2010 2/16= 0.13 a
Comparison	Difference	SE	q	q
2008 vs 2007	22.79-12.92=9.87	2.74	3.6	3.63
GUILD C	2007 75/288=0.26 a	2008 14/67=0.21 a	2009 20/102=0.21 a	2010 3/16= 0.19 a
Comparison	Difference	SE	Q	q
2007 vs 2010	30.66-25.84=4.84	5.12	0.95	3.63
GUILD D	2007 61/288=0.21 a	2008 11/67=0.16 a	2009 24/102=0.24 a	2010 3/16= 0.19 a
Comparison	Difference	SE	q	q
2009 vs 2008	29.33-23.58=5.75	3.17	1.81	3.63
GUILD E	2007 2/288=0.03 b	2008 0 a	2009 3/102=0.03 b	2010 0 a
Comparison	Difference	SE	q	q
2009 vs 2008	9.97-0=9.97	1.81	5.51	3.63
2009 vs 2007	9.97-4.8=5.17	2.33	2.21	3.63

Appendix D

Table 18- Standard error calculations for multiple comparison test of proportions for sites at Pinery: (a) fresh site, (b) intermediate site, (c) mature site, (d) control site.

(a) fresh site

Comparison	Step 1	Step 2	SE
2008 vs 2010	$(\sqrt{(410.35/200.5)+(410.35/377.5)})$	$(\sqrt{(2.05 + 1.09)})$	1.77
2008 vs 2007	$(\sqrt{(410.35/200.5)+(410.35/1013.5)})$	$(\sqrt{(2.05 + 0.405)})$	1.57
2009 vs 2007	$(\sqrt{(410.35/1013.5)+(410.35/1012.5)})$	$(\sqrt{(0.40 + 0.405)})$	0.90
2007 vs 2010	$(\sqrt{(410.35/1013.5)+(410.35/377.5)})$	$(\sqrt{(0.405 + 1.09)})$	1.22
2009 vs 2008	$(\sqrt{(410.35/1013.5)+(410.35/200.5)})$	$(\sqrt{(0.40 + 0.41)})$	1.57
2010 vs 2009	$(\sqrt{(410.35/1013.5)+(410.35/1012.5)})$	$(\sqrt{(0.40 + 0.405)})$	0.9

(b) intermediate site

Comparison	Step 1	Step 2	SE
2007 vs 2008	$(\sqrt{(410.35/1019.5)+(410.35/1468.5)})$	$(\sqrt{(0.403 + 0.28)})$	0.826
2007 vs 2009	$(\sqrt{(410.35/1019.5)+(410.35/883.5)})$	$(\sqrt{(0.403 + 0.464)})$	0.931
2007 vs 2010	$(\sqrt{(410.35/1019.5)+(410.35/770.5)})$	$(\sqrt{(0.404 + 0.533)})$	0.967
2008 vs 2009	$(\sqrt{(410.35/883.5)+(410.35/1468.5)})$	$(\sqrt{(0.464 + 0.28)})$	0.862
2008 vs 2010	$(\sqrt{(410.35/883.5)+(410.35/770.5)})$	$(\sqrt{(0.464 + 0.533)})$	0.998
2009 vs 2010	$(\sqrt{(410.35/1468.5)+(410.35/770.5)})$	$(\sqrt{(0.28 + 0.533)})$	0.902

(c) mature site

Comparison	Step 1	Step 2	SE
2010 vs 2009	$(\sqrt{(410.35/178.5)+(410.35/307.5)})$	$(\sqrt{(2.30 + 1.33)})$	1.91
2010 vs 2007	$(\sqrt{(410.35/178.5)+(410.35/573.5)})$	$(\sqrt{(2.30 + 0.716)})$	1.74
2010 vs 2008	$(\sqrt{(410.35/178.5)+(410.35/786.5)})$	$(\sqrt{(2.30 + 0.52)})$	1.68
2008 vs 2007	$(\sqrt{(410.35/786.5)+(410.35/573.5)})$	$(\sqrt{(0.52 + 0.716)})$	1.11
2007 vs 2009	$(\sqrt{(410.35/573.5)+(410.35/307.5)})$	$(\sqrt{(0.716 + 1.33)})$	1.43
2008 vs 2009	$(\sqrt{(410.35/786.5)+(410.35/307.5)})$	$(\sqrt{(0.52 + 1.33)})$	1.36

(d) control site

Comparison	Step 1	Step 2	SE
2010 vs 2009	$(\sqrt{(410.35/495.5)+(410.35/1251.5)})$	$(\sqrt{(0.82 + 0.327)})$	1.075
2007 vs 2009	$(\sqrt{(410.35/1251.5)+(410.35/1127.5)})$	$(\sqrt{(0.3279 + 0.3639)})$	0.8317
2009 vs 2008	$(\sqrt{(410.35/1251.5)+(410.35/829.5)})$	$(\sqrt{(0.3279 + 0.4947)})$	0.9070
2007 vs 2010	$(\sqrt{(410.35/1127.5)+(410.35/495.5)})$	$(\sqrt{(0.3636 + 0.8282)})$	1.092
2007 vs 2008	$(\sqrt{(410.35/1127.5)+(410.35/829.5)})$	$(\sqrt{(0.3636 + 0.4947)})$	0.927
2008 vs 2010	$(\sqrt{(410.35/829.5)+(410.35/495.5)})$	$(\sqrt{(0.4947 + 0.828)})$	1.15

Table 19- Standard error calculations for multiple comparison test of proportions for sites at Turkey Point: (a) fresh site, (b) intermediate site, (c) mature site, (d) control site.

(a) fresh site

Comparison	Step 1	Step 2	SE
2009 vs 2008	$(\sqrt{(410.35/126.5)+(410.35/26.5)})$	$(\sqrt{(3.24 + 15.48)})$	4.3
2008 vs 2007	$(\sqrt{(410.35/26.5)+(410.35/149.5)})$	$(\sqrt{(15.48 + 2.74)})$	4.27
2010 vs 2009	$(\sqrt{(410.35/40.5)+(410.35/126.5)})$	$(\sqrt{(10.13 + 3.24)})$	3.66
2010 vs 2007	$(\sqrt{(410.35/40.5)+(410.35/149.5)})$	$(\sqrt{(3.24 + 2.74)})$	2.44

(b) intermediate site

Comparison	Step 1	Step 2	SE
2007 vs 2009	$(\sqrt{(410.35/262.5)+(410.35/835.5)})$	$(\sqrt{(1.56 + 0.49)})$	1.43
2008 vs 2009	$(\sqrt{(410.35/315.5)+(410.35/835.5)})$	$(\sqrt{(1.3 + 0.49)})$	1.39
2010 vs 2008	$(\sqrt{(410.35/397.5)+(410.35/315.5)})$	$(\sqrt{(1.03 + 1.3)})$	1.53
2007 vs 2008	$(\sqrt{(410.35/262.5)+(410.35/315.5)})$	$(\sqrt{(1.56 + 1.3)})$	1.69
2007 vs 2010	$(\sqrt{(410.35/262.5)+(410.35/397.5)})$	$(\sqrt{(1.56 + 1.03)})$	1.61

(c) mature site

Comparison	Step 1	Step 2	SE
2008 vs 2007	$(\sqrt{(410.35/199.5)+(410.35/595.5)})$	$(\sqrt{(2.6 + 4.12)})$	2.59
2007 vs 2010	$(\sqrt{(410.35/95.5)+(410.35/100.5)})$	$(\sqrt{(4.29 + 4.08)})$	2.89
2007 vs 2009	$(\sqrt{(410.35/95.5)+(410.35/164.5)})$	$(\sqrt{(4.30 + 2.49)})$	2.61
2009 vs 2008	$(\sqrt{(410.35/164.5)+(410.35/199.5)})$	$(\sqrt{(2.49 + 2.06)})$	2.13

(d) control site

Comparison	Step 1	Step 2	SE
2008 vs 2007	$(\sqrt{(410.35/67.5)+(410.35/288.5)})$	$(\sqrt{(6.08 + 1.44)})$	2.59
2007 vs 2010	$(\sqrt{(410.35/288.5)+(410.35/16.5)})$	$(\sqrt{(1.42 + 24.87)})$	5.12
2009 vs 2008	$(\sqrt{(410.35/102.5)+(410.35/67.5)})$	$(\sqrt{(4.00 + 6.08)})$	3.17
2009 vs 2007	$(\sqrt{(410.35/102.5)+(410.35/288.5)})$	$(\sqrt{(4.00 + 1.42)})$	2.33

Appendix E

Single season output example from PRESENCE software
PRESENCE - Presence/Absence-Site Occupancy data analysis

Thu Nov 29 13:44:28 2012, Version 2.4090918

==>i=c:\users\user\documents\phd
dissertation\phd!!!!\agapostemonsplendenspinery2007_project\agapostemonsplendenspin
ery2007_project\agapostemonsplendenspinery2007.pao

==>l=c:\users\user\documents\phd
dissertation\phd!!!!\agapostemonsplendenspinery2007_project\agapostemonsplendenspin
ery2007_project\agapostemonsplendenspinery2007.pa3.out

==>name=agapostemonsplendenspinery2007psi(site),p(site)

==>model=1

==>j=c:\users\user\documents\phd
dissertation\phd!!!!\agapostemonsplendenspinery2007_project\agapostemonsplendenspin
ery2007_project\agapostemonsplendenspinery2007.dm

==>lmt=200

model=1 N,T-->19,10

modtype-->1 Single-Season data Model selected

Data checksum = 52516

NSi-->1

site_covname[0]=fire

NSa-->0

agapostemonsplendenspinery2007

modtype=1 N=19 T=10 Groups=1 bootstraps=0

-->1-10

Matrix 1: rows=2, cols=2

-,a1,

psi 1

=====

Matrix 2: rows=11, cols=11

-,b1,b2,b3,b4,b5,b6,b7,b8,b9,b10,

p1 1 0 0 0 0 0 0 0 0 0 0

p2 0 1 0 0 0 0 0 0 0 0 0

p3 0 0 1 0 0 0 0 0 0 0 0

p4 0 0 0 1 0 0 0 0 0 0 0

p5 0 0 0 0 1 0 0 0 0 0 0

p6 0 0 0 0 0 1 0 0 0 0 0

p7 0 0 0 0 0 0 1 0 0 0 0

p8 0 0 0 0 0 0 0 1 0 0 0

p9 0 0 0 0 0 0 0 0 1 0 0

p10 0 0 0 0 0 0 0 0 0 1 0

=====

Custom Model:

Number of sites = 19

Number of sampling occasions = 10

Number of missing observations = 0

Number of parameters = 11

Number of significant digits = 7.6

Number of function calls = 541

-2log(likelihood) = 169.4198

AIC = 191.419772

Model has been fit using the logistic link.

Naive estimate = 0.9474

Untransformed Estimates of coefficients for covariates (Beta's)

=====

estimate std.error

A1	:occupancy	psi	4.441160 (5.050654)
B1	:detection	p1	-2.126966 (0.750437)
B2	:detection	p2	-20.012404 (2138.091392)
B3	:detection	p3	0.346500 (0.485809)
B4	:detection	p4	-2.878004 (1.029279)
B5	:detection	p5	-0.756024 (0.501052)
B6	:detection	p6	-1.013689 (0.527114)
B7	:detection	p7	0.130252 (0.476343)
B8	:detection	p8	-0.756024 (0.501052)
B9	:detection	p9	-2.878004 (1.029279)
B10	:detection	p10	-1.306896 (0.567670)

Variance-Covariance Matrix of Untransformed estimates (Beta's):

	A1	B1	B2	B3	B4	B5	B6	B7	B8	B9
B10										
A1	25.509102	-0.272898	-0.022414	-0.588565	-0.257573	-0.358282	-0.332284	-0.521520	-0.358282	-0.257573
B1	-0.272898	0.563156	0.000290	0.007672	0.003357	0.004670	0.004331	0.006798	0.004670	0.003357
B2	-0.022414	0.000290	4571434.800520	0.000629	0.000277	0.000380	0.000356	0.000559	0.000385	0.000277
B3	-0.588565	0.007672	0.000629	0.236010	0.007241	0.010072	0.009341	0.014661	0.010072	0.007241
B4	-0.257573	0.003357	0.000277	0.007241	1.059416	0.004408	0.004088	0.006416	0.004408	0.003169
B5	-0.358282	-0.257573	-0.309806							
B6	-0.332284	0.004331	0.004038							
B7	-0.521520	0.006798	0.004038							
B8	-0.257573	0.003357	0.000277							
B9	-0.257573	0.003357	0.000277							

B5 -0.358282 0.004670 0.000380 0.010072 0.004408 0.251053 0.005686
0.008925 0.006131 0.004408 0.005302

B6 -0.332284 0.004331 0.000356 0.009341 0.004088 0.005686 0.277849
0.008277 0.005686 0.004088 0.004917

B7 -0.521520 0.006798 0.000559 0.014661 0.006416 0.008925 0.008277
0.226903 0.008925 0.006416 0.007717

B8 -0.358282 0.004670 0.000385 0.010072 0.004408 0.006131 0.005686
0.008925 0.251053 0.004408 0.005302

B9 -0.257573 0.003357 0.000277 0.007241 0.003169 0.004408 0.004088
0.006416 0.004408 1.059416 0.003811

B10 -0.309806 0.004038 0.000330 0.008709 0.003811 0.005302 0.004917
0.007717 0.005302 0.003811 0.322249

=====

Individual Site estimates of Psi:

Site	Survey	Psi	Std.err	95% conf. interval
1 NSITECOV:0	1	1-1:	0.9884	0.0581 0.0042 - 1.0000

=====

Individual Site estimates of p:

Site	Survey	p	Std.err	95% conf. interval
1 NSITECOV:0	1	1-1: 0.1065	0.0714	0.0267 - 0.3416
1 NSITECOV:0	2	1-2: 0.0000	0.0000	0.0000 - 1.0000
1 NSITECOV:0	3	1-3: 0.5858	0.1179	0.3530 - 0.7856
1 NSITECOV:0	4	1-4: 0.0533	0.0519	0.0074 - 0.2972
1 NSITECOV:0	5	1-5: 0.3195	0.1089	0.1496 - 0.5563
1 NSITECOV:0	6	1-6: 0.2663	0.1030	0.1144 - 0.5049
1 NSITECOV:0	7	1-7: 0.5325	0.1186	0.3093 - 0.7434
1 NSITECOV:0	8	1-8: 0.3195	0.1089	0.1496 - 0.5563
1 NSITECOV:0	9	1-9: 0.0533	0.0519	0.0074 - 0.2972
1 NSITECOV:0	10	1-10: 0.2130	0.0952	0.0817 - 0.4516

Distribution of p's:

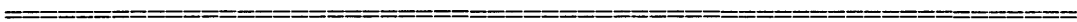
```

0.00 19:*****
0.03 0:
0.05 38:*****
0.07 0:
0.10 19:*****
0.13 0:
0.15 0:
0.17 0:
0.20 19:*****

```

0.23 0:
0.25 19:*****
0.28 0:
0.30 38:*****
0.33 0:
0.35 0:
0.38 0:
0.40 0:
0.42 0:
0.45 0:
0.47 0:
0.50 0:
0.53 19:*****
0.55 0:
0.57 19:*****
0.60 0:
0.63 0:
0.65 0:
0.68 0:
0.70 0:
0.72 0:
0.75 0:

0.78 0:
 0.80 0:
 0.82 0:
 0.85 0:
 0.88 0:
 0.90 0:
 0.93 0:
 0.95 0:
 0.97 0:
 1.00 0:



DERIVED parameter - Psi-conditional : [Pr(occ | detection history)]

Site	psi-cond	Std.err	95% conf. interval
1 NSITECOV:0	1.0000	0.0000	1.0000 - 1.0000
2 site 2	1.0000	0.0000	1.0000 - 1.0000
3 site 3	1.0000	0.0000	1.0000 - 1.0000
4 site 4	1.0000	0.0000	1.0000 - 1.0000
5 site 5	1.0000	0.0000	1.0000 - 1.0000

6	site 6	1.0000	0.0000	1.0000 - 1.0000
7	site 7	1.0000	0.0000	1.0000 - 1.0000
8	site 8	1.0000	0.0000	1.0000 - 1.0000
9	site 9	1.0000	0.0000	1.0000 - 1.0000
10	site 10	1.0000	0.0000	1.0000 - 1.0000
11	site 11	1.0000	0.0000	1.0000 - 1.0000
12	site 12	1.0000	0.0000	1.0000 - 1.0000
13	site 13	1.0000	0.0000	1.0000 - 1.0000
14	site 14	0.7787	0.9099	-1.0046 - 2.5621
15	site 15	1.0000	0.0000	1.0000 - 1.0000
16	site 16	1.0000	0.0000	1.0000 - 1.0000
17	site 17	1.0000	0.0000	1.0000 - 1.0000
18	site 18	1.0000	0.0000	1.0000 - 1.0000
19	site 19	1.0000	0.0000	1.0000 - 1.0000

CPU time: 0.0 seconds