Land-use Change and the Decline of the Western Bumble Bee

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Abstract of Thesis

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Recent studies have documented a drastic decline in managed honey bee colonies (termed Colony Collapse Disorder), and in an attempt to catalogue the current status of native pollinator communities, successive research has inadvertently revealed a parallel decline. Of interest for the present study, researchers reported in 2010 that populations of North American bumble bees, Bombus spp., are in steep decline. While many unique North American bumble bee species exist, all share similar natural history traits and significantly contribute to the maintenance of local biodiversity through their pollination services. The present study focuses on the decline of B. occidentalis, a bumble bee with an historic range throughout the western United States. Maxent, a presence-only species distribution modeling (SDM) program, was used to measure the impact of land-use change from 1992 to 2006 on the recent decline of B. occidentalis in the state of Oregon. Analysis and measurement of the projections revealed that land-use change has not been a driver of the decline in B. occidentalis populations; conversely, land-use change, theoretically, should have allowed for the geographical expansion of B. occidentalis populations, thereby suggesting that other factors, such as agricultural intensification, use of neonicotinoids, and fungal parasites, are responsible. The present study concludes that the suitability of a given location for B. occidentalis can be significantly predicted via proximity to natural habitat and floral resources. Optimally, the distances to nesting habitat and floral resources should be no greater than 5 km and 1 km, respectively.
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Chapter 1: Natural History, Importance, and Conservation Status of Bumble Bees

Introduction

The ecosystem service provided by pollinators is economically and ecologically crucial, and it significantly contributes to the production of a nutritious diet for humans (Eilers et al. 2011) while fostering tremendous local biodiversity (Biesmeijer et al. 2006). Almost all fruits, cucurbits, and nuts that are farmed commercially rely directly on pollination for production, and many sources of food stock in the ranching industry indirectly rely on insect-pollinated plants. If both direct and indirect agricultural contributions are considered together, roughly one-third of all food consumed worldwide depends on insect pollination. At a broader scale, when all contributions, both to agricultural productivity and maintenance of biodiversity, are combined, the global monetary value of wild insect pollinators has been estimated to be at least $216 billion (Chaplin-Kramer et al. 2011).

The ecological relationship between insect pollinators and their respective plants are often mutualistic, but in many cases, the plant ‘directs’ the process. For example, by producing showy flowers, sugary nectar, and abundant pollen used as a protein source for their young, the plant entices local bees to forage proximally to its pollen-producing anthers. As the bee actively collects nectar and pollen from the flower, it becomes coated with pollen, and the bee inadvertently transports the pollen from the anther of one flower to the stigma of another as it continues foraging. Taken together, the pollinator receives
nutritional supplies, while the plant receives reproductive aid; therefore, a crucial resource is provided for both parties.

The current standard for commercial pollination is the honey bee. In recent years, a phenomenon termed Colony Collapse Disorder (CCD) has decimated honey bee hives worldwide (vanEngelsdorp et al. 2011). While various factors, such as an infestation of varroa mites and the subsequent exposure to miticide, can lead to routine hive loss, CCD is characterized by unexplained, instantaneous loss of a significant percentage of managed hives. Researchers have proposed a few causes (pathogens, neonicotinoids, loss of genetic diversity, and land-use), but to-date, no ‘smoking gun’ discovery has fully explained the rate of hive loss. Nevertheless, commercially managed honey bee hives are disappearing world-wide at an alarming rate. Because there seems to be no quick cure, CCD has the potential to severely impact industrialized agriculture, and the phenomenon has prompted researchers to investigate the pollination efficiency (i.e., the ability to replace the honey bee) and availability of resident native pollinators.

While the honey bee is actively managed in agricultural settings, recent research suggests that over 60% of all agricultural pollination is actually performed by native bees; of those native pollinators, the bumble bee, Bombus spp., is the most important (Winfree et al. 2011). Because of their potential agricultural contribution, the US monetary value of native bees has been estimated at roughly $3 billion (Losey and Vaughan 2006). Similarly, their importance for maintenance of biodiversity is so great that a local decline
of native bees has been shown to be significantly correlated to the decline of local plants that directly rely on their pollination services (Biesmeijer et al. 2006).

In some cases, bumble bees are arguably more important than honey bees for the maintenance of local biodiversity and commercial farming enterprises (Ollerton et al. 2012). In the UK, the percentage of land used for insect-pollinated commercial crops has grown beyond the pollination capabilities of honey bees, yet yields in the region have remained roughly constant, suggesting that native bee populations are capable of fulfilling the remaining ecosystem service (Breeze et al. 2011). Due to this finding, scientists currently disagree as to whether CCD should even be included in the greater discussion of pollinator decline (i.e., should honey bees play the central role in raising awareness of pollinator decline when the presence of native bees has been found to be of equal or greater importance?) (Ollerton et al. 2012). While rebuttals have been put forth that suggest that the scientific community should include honey bees in the greater conversation (Aebil et al. 2012), the overall importance of bumble bees and native pollinators seems too great to be overshadowed by the loss of an exotic, commercial pollinator that some studies suggest does not pollinate as efficiently as native bees.

Like the honey bee, wild bees (including *Bombus* spp.) have been shown to be in steep decline. Various, commonly-recognized North American species have potentially gone extinct (e.g., *B. franklini*), and others have suffered declines in their population sizes and ranges (e.g., *B. terricola, B. occidentalis, B. pensylvanicus* and *B. affinis*) (Cameron et al. 
2011). Causes, again, potentially include pathogens, pesticide use, loss of genetic diversity, and land-use change.

To the author’s knowledge, no previous study has attempted to measure the impact of land-use change on *Bombus* spp. by combining geographic information systems (GIS) and species distribution models (SDM). Specifically the present study focuses on the impact that land-use change from 1992 to 2006 in the state of Oregon may have had on the western bumble bee, *B. occidentalis*.

**Natural History**

The bumble bee is an important pollinating insect that exhibits eusocial behavior by means of reproductively-defined labor, multiple contemporaneous generations, and joint tending of the young (Gadagkar 1993). Normally, colonies are found in or on the ground in existing cavities (e.g., vacant rodent burrows) (McFrederick and LeBuhn 2006), but they rarely persist through the winter. Because of this attribute, new colonies are founded early each spring by individual, fertilized queens that have successfully over-wintered. Within a few weeks of its founding, and assuming the queen is able to locate sufficient resources, the colony expands, and workers begin to assume foraging and maintenance responsibilities. While mature colony size is species-dependent, rarely do colonies grow larger than a few hundred workers.
Bumble bees are holometabulous insects, meaning that they fully pass through four stages in their development: egg, larva, pupa, and adult. Almost all initial eggs laid by the queen are fertilized, so they emerge as female workers. However, as the colony ages, the queen loses the ability to hormonally suppress other female workers in the hive; they too begin to lay eggs, all of which are unfertilized and become male drones. Before the end of the flowering season, multiple reproductives (i.e., drones and new queens) are produced. To search for reproductive partners, the new queens (gynes) voluntarily leave the hive, while the male drones are forced out. Ideally, to reduce inbreeding depression, a male and female from unique colonies mate, and, following fertilization, the queen searches for a suitable site to over-winter. The following spring, she re-emerges to found a new colony.

For sustenance, mature bumble bees collect the nectar of flowering plants. In rare occasions, or if the resource is especially rich, bees may fly more than 1.5 km from their nest in search of floral resources (Walther-Hellwig and Frankl 2000). However, the developing larvae within the colony need more nutrients than nectar can provide, so foragers also collect protein-rich pollen. By feeding on such floral resources, bumble bees incidentally offer tremendous pollination services to hundreds of flowering plant species (Colla, S.R., and S. Dumesh 2010).

Interestingly, while the honey bee may be the choice for much of the agricultural industry, it’s possible that the bumble bee may be a significantly better pollinator (Stubbs and Drummond 2001). Recently, agriculturalists have begun to take advantage of a
unique ability of some bumble bees: ‘buzz pollination’. The frequency at which some bumble bees vibrate their wings matches the frequency necessary to release pollen from tomato flowers, so some species (e.g., *B. impatiens* and *B. occidentalis*) are now commercially reared for greenhouse tomato production (Velthuis and van Doorn 2006). Generally, *Bombus* spp. tends to pollinate more efficiently than *Apis mellifera* (Holzschuh et al. 2012) and produce a greater fruit set and weight in a shorter period of time (Artz and Nault 2011). Additionally, it has been suggested that bumble bees are particularly strong performers in berry and cucurbit crops (Adamson et al. 2012). In fact, their performance warrants the argument that local bumble bees should be preferred to managed honey bee hives in the commercial production of these two crops. However, this suggestion begs the question of whether bumble bees can be commercially managed like honey bees.

Bumble bees have had a long history of attempted domestication. Much advancement has been made, ultimately providing a few situations in which commercial bumble bees can be used in place of honey bees (Velthuis and van Doorn 2006). However, due to the limited size of their colonies, it is unlikely that bumble bees will ever reach the level of ‘industrialization’ seen in honey bees.

If bumble bees cannot be industrialized and transported at the same scale as honey bees, use of bumble bees as commercial pollinators must begin with large, healthy populations within the immediate vicinity of the crop in question. Although a few studies suggest otherwise (Winfrey et al. 2008), most researchers agree that proximity to natural habitat
and favorable land-use practices strongly influence the presence and size of local bumble bee populations. Kremen et al. (2002) measured the abundance and diversity of native bees on various types of farms and found that to fulfill all necessary pollination requirements, native bees were sufficiently abundant only at organic farms; at other locations, farming intensification, monocropping, and land-use practices negatively impacted pollinator presence. Similarly, Garibaldi et al. (2011) found that as quantities of surrounding natural habitat decline, native pollinators and crop productivity significantly decline, regardless of the abundance of managed honey bees. At a very local scale, Shuler et al. (2005) found that tillage practices negatively impacted local pollinator levels. If farmers desire to replace costly, at-risk honey bee hives with inexpensive, local bumble bees, a stronger effort must be made to maintain, or reintroduce if necessary, natural habitats that provide nesting ground and a variety of dietary options conducive to wild bumble bee colony maintenance.

Interestingly, two studies suggest contradictory results when both *Bombus* spp. and *A. mellifera* are used in tandem for pollination. Goulson and Sparrow (2009) found that the mean size of the *Bombus* spp. thorax was significantly smaller in the presence of managed honey bee hives, suggesting strong resource competition between the two groups. Should a thriving local bumble bee population be desired, conservation efforts might begin to include restrictions on allowable locations of managed honey bee hives to reduce strain on the local pollinator community. On the other hand, Greenleaf and Kremen (2006) found that, when the two are combined, the behavior of both groups changes in such a way as to increase the overall pollination efficiency; in fact, the
researchers stress that the impact is so significant that the indirect effect of mutual presence is five times more meaningful than the direct pollination contribution by bumble bees. Therefore, if we consider these two studies together, it can be inferred that while farm yields might be boosted in the short-term from having both types of pollinators present, the overall fitness of bumble bee populations would suffer in the long-term due to resource competition.

In contrast to the two aforementioned studies, a notable study by Lye et al. (2011) suggests that if *Bombus* spp. is not present in the local wild pollinator community, the introduction of commercial *Bombus* spp. nests will not detrimentally impact the abundance and diversity of the local pollinator community but will significantly increase crop yield. On balance, the introduction of *Bombus* spp. will likely increase crop yield without detrimentally impacting native pollinator communities, but more research is necessary

**Conservation Status of Bumble Bees**

**Wild Populations**

The decline of bumble bee populations gained the full attention of scientists following the collapse of commercial honey bee hives (vanEngelsdorp et al. 2007). Consequent field studies of bumble bees in Britain revealed that 2 of 24 known species had disappeared and eight were in serious decline (Williams and Osborne 2009). Once word spread of the
severe decline, North American scientists looked for and found a similar pattern in native bumble bee communities. One study shows that *B. terricola, B. occidentalis, B. pensylvanicus* and *B. affinis* are each in steep decline, while at least one species, *B. impatiens*, appears to have expanded its range (Cameron et al. 2011). Another study suggests that at least one species, *B. franklini*, may already be extinct (Thorp 2005). Unfortunately, a general lack of detailed records for many of the 46 species found in North America obscures the overall status of North American bumble bees. However, due to their contribution to agriculture and biodiversity, any significant decline of North American bumble bee species is cause for concern.

A wide range of threats appears to be putting many North American bumble bees at risk. Some threats appear to impact local populations in a very protracted manner (agricultural intensification, altered land-use patterns, general habitat fragmentation, and climate change), while other threats seem much more acute (neonicotinoid insecticides and *Nosema bombi*, a fungal parasite).

**Protracted Threats**

Agricultural intensification is a common phenomenon in which a farming landscape slowly becomes more industrialized. Techniques that more closely represent natural biological patterns are abandoned for mechanization and petroleum-based applications. As intensification progresses, a single farm can expand from a local, family-owned plot to a large mono-crop system. In the slow process of aggregating small plots into a large,
more uniform expanse, the diversity of agricultural crops often significantly decreases and the distance between surrounding floral resources that bumble bees might utilize significantly increases (Kleijn and Raemakers 2008). Numerous studies have linked this process to an overall decline in abundance and diversity of bumble bees (Grixti et al. 2009; Williams and Osborne 2009). In the most basic sense, floral resource abundance and diversity can be thought of as the single most important habitat feature for bumble bees, and while a large mono-crop system may have sufficient surrounding floral resources for a few colonies, it does not lend itself well to sustaining large populations, particularly when the crops are not animal-pollinated.

Even if the local landscape were to provide sufficient floral resource abundance and diversity, it still remains that land-use itself may prevent sustainable populations of bumble bees. It appears difficult to reach a consensus on the issue of tillage, but studies directed at other invertebrates have demonstrated that the practice in general was detrimental (Kladivko 2001). Because bumble bees often nest in or on the ground, it has been suggested that tillage can significantly impact the success of colonies by potentially killing mature bees and exposing larvae to predators and detrimental environmental conditions. Overall, with very few studies on available nesting sites and the subsequent impact on bee populations, it is difficult to determine the degree to which mechanized soil disturbance is significantly contributing to the decline.

In a general sense, habitat fragmentation is thought to play an underlying role in the decline of North American bumble bees (Cane 2001). Normally, habitat fragmentation is
defined as the anthropogenically-induced destruction of natural habitat and the resulting change of its spatial attributes. A viable habitat is reduced in its overall size and split into smaller, disjointed patches, significantly reducing the interior-to-edge ratio. Populations of a given species may become isolated in these narrow bands of habitat as the matrix between patches becomes more commercially developed, thereby reducing effective population sizes, diminishing inter-population migration, and impacting its genetic heterozygosity (Saunders et al. 1991). Over time, these changes can negatively impact a species’ fitness and increase the likelihood of future extinction. The chance of stochastic extinction in fragments greatly increases with habitat fragmentation (Groom et al. 2005).

However, while many species are severely impacted by these increasingly small, isolated patches, bumble bees seem to react a bit differently. Floral resources tend to be greater in ecologically disturbed, sunny plots, and the necessary habitats for ground nesting tend to be associated with respective habitat edges, such as those found around agricultural plots (Svensson et al. 2000). For example, it has been shown that logged areas, which often have many flower outcrops, can sustain large bee populations (Romey et al. 2007). So an area that may qualify as fragmented for many species may be beneficial for the local bumble bee populations. That being said, it is still difficult to conclude that habitat fragmentation on a large scale would not detrimentally impact bumble bee populations. As previously mentioned, while certain fragmented habitats may appear beneficial, once a threshold of floral resource reduction and loss of proper nesting habitat has been reached (i.e., the balance of habitat types is no longer favorable), bumble bee species may begin to suffer (Laurance et al. 2011).
Climate change may also impact the floral resources available to bumble bees. Global temperature changes are likely to impact precipitation patterns (Hurrell 1995). As a result, floral flushes may be temporally impacted (Levine et al. 2011). While few studies have directly tested the impact on pollinator communities, it seems logical that environmental changes that significantly alter the availability of floral resources may contribute to the decline of pollinator populations.

*Acute Threats*

*Nosema bombi*, a fungal parasite found in the digestive tract of bumble bees, is arguably the largest threat to wild bumble bee populations. It appears that the infection most significantly manifests itself in commercially reared colonies, but the disease has the potential for escaping the confines of a commercial greenhouse and infecting local wild populations (Colla et al. 2006). Because bumble bees are incapable of trophallaxis (i.e., direct transfer of food between individuals), transmission appears to be indirect (i.e., when a wild bee visits a flower previously visited by an infected bee). Unfortunately, because of its nature, no management strategy can sufficiently address the issue aside from suggesting that commercially-reared populations be diligently monitored and isolated when the fungus presents itself.

In many managed landscapes, pesticide/insecticide use is common practice. A recent study suggests that neonicotinoids, in particular, are harmful. Although all bees of a single colony may not consume lethal doses of the substance, elongated exposure may
cause noticeable changes in foraging habits and disorientation (Henry et al. 2012) and an overall decrease in fitness and development of the colony (Whitehorn et al. 2012). Just as the management of Nosema bombi is little more than a recommendation, so too is the suspension of neonicotinoids. If their use is to be banned, that mandate must come from a state or federal legislative body.

**Implications for Present Study**

The important ecological role played by bumble bees cannot be overvalued. The worrisome decline of many historically-abundant species has prompted the scientific community to begin studying many factors that now appear to be principal causes of the phenomenon. As previously mentioned, the fungal parasite Nosema bombi and the use of neonicotinoid parasites are currently two of the more worrisome threats to North American bumble bee species. However, evaluation of the other potential threats is certainly worthwhile. By rigorously testing, and potentially rejecting, each mechanism for its role in the recent decline, the confidence with which a diagnosis can be applied to the observed decline is significantly increased.
Chapter 2: Original Research

Methods

The overall aim of the present study was to measure the impact that land-use change from 1992 to 2006 potentially had on the decline of the western bumble bee, *Bombus occidentalis*. Oregon was selected as the geographical study area. Three factors drove that decision: previous research suggested that Oregon has experienced a significant decline in populations of *B. occidentalis*; the size of Oregon significantly reduced the size of all rasters and shapefiles (and therefore reduced the required computational power); and, because land-use rasters of Canada and Mexico were not used in the present study, a geographical area that does not share a border with either country was required to properly calculate the Euclidean distance to each land-use plot.

Maxent, a presence-only species distribution modeling (SDM) program, was used to create projections of the realized niche of *B. occidentalis* in Oregon in both 1992 and 2006. The Maxent projections were imported into ArcGIS 10.1 to measure the change in the area of suitable habitat that occurred between these dates when both bioclimatic and land-use variables were used to generate the SDMs. All other Maxent outputs were analyzed to explore potential relationships between suitable habitat and land-use categories that might be informative for conservation purposes.
Prior to the creation of the SDM, pollinator sampling data (provided by Cameron et al.; hereafter ‘sampling points’) were cleaned and prepared such that only unique sample points collected between 2004-2008 across the western half of the United States were included in the model. Because land-use presumably did change between 1992 and 2006, all *B. occidentalis* sample points used to create the SDM must originate from a single time frame, 1990-1994 or 2004-2008 (the selected 4-year time frames bracket each ‘target year’ and were chosen to ensure an adequate sample size). Sample points collected during 2004-2008 were used because that time frame offered more unique sample points (by coordinates). A single model was created and subsequently projected onto separate land-use maps for Oregon in 1992 and 2006.

To better represent the surrounding environment of each sample point, the categorical data associated with the original land-use map (NLCD 2006, 30m resolution) was converted to continuous data. The original categorical map was converted to four shapefiles, with each shapefile representing a certain land-use category: ‘forest’, ‘open to medium development’ (open-med), ‘shrub and grassland’ (shrub-grass), and ‘pasture and cropland’ (past-crop). These shapefiles were then used to calculate the distance from each sample point to the nearest plot of each land-use category. In other words, rather than assigning a single, categorical variable for each sample point that identifies the type of land from which it was collected, four variables were created that quantify the distance from the sample point to the closest plot of the aforementioned categories. In theory, the conversion from categorical to continuous data should therefore better represent the immediate environment of the sample points.
Because Maxent creates models by using presence-only data, it is necessary to include background points that create a framework for the sample point data. Originally, 10,000 random background points across the western half of the United States were created, but due to limitations of and glitches in the ArcGIS software, the data for only 9,544 points were successfully extracted and included in the final model. Using the land-use shapefiles from 2006, distance was calculated from each background point to the nearest plot of each land-use category.

Only the ‘current’ (average from 1950-2000) bioclimatic variables used by Cameron et al. (2010) were included in the present study: Bio1 - Bio6, Bio8, Bio9, Bio12, Bio14, Bio15, and Bio18 (see Table 1 for explanations); according to Cameron et al., when the absolute correlation coefficient between two variables was greater than or equal to 0.90, only one variable was included. Otherwise, both variables were included. Using ArcMap 10.1, bioclimatic values were extracted for all sample and background points.

Ultimately, the 50 sample points (all collected from 2004-2008) and 9,544 random background points (which theoretically represent the possible habitats in 2006) were used to create an Oregon-specific SDM in Maxent 3.3.3k using ‘samples with data’ (SWD) format, and the model was projected onto 1992 and 2006 land-use coverages. For the present study, the selected regularization parameter value (3) provided the greatest overall AUC when compared to other values (for all parameters, see Appendix).
The final Maxent projections were imported into ArcMap 10.1. Each projection raster was reclassified to a binary format (suitable=1, unsuitable=0) by using the ‘minimum training presence’ as the threshold. The area of land predicted as suitable habitat for *B. occidentalis* was calculated and compared between 1992 and 2006. Because the threshold between suitable and unsuitable habitat is based on the probabilities assigned to the sample points used to create the model, the distinction is not arbitrary.

All MaxEnt output parameters (AUC, omission rate, jackknife, response curves, and percent contribution/permutation importance) were evaluated to determine the overall model significance and the contribution of each land-use category. Because the values of all bioclimatic variables were identical for both projections, they could not contribute to any change in the area of land predicted as suitable habitat. Additionally, because the present study was solely interested in the impact of land-use change, no evaluation of the importance of the bioclimatic variables was conducted for the present study. Where possible, and in conjunction with specific *Bombus* spp. natural history traits, Maxent output was interpreted for conservation uses.

*Analytical Methods*

Maxent is a presence-only species distribution modeling program. In short, Maxent calculates the probability of suitable habitat for a species, given a user-specified geographical range and set of environmental variables. The probability is determined by applying the theory of maximum entropy (i.e., a dataset with an unknown distribution
should have no arbitrary constraints added; Phillips et al. 2006) to environmental data associated with the geographically-referenced sample points. Because the program is presence-only, Maxent is only able to extrapolate to novel locations by referencing the sample data against random background points that also carry relevant environmental data. The final model is created by taking into account both sample and background points, and the model can then be projected, with caution, either to a unique set of environmental data, as seen in the present study, or to a future scenario (e.g., climate change).

In order to determine the significance of the model and the contribution of each environmental variable, Maxent produces various measures of fit: area under the curve (AUC), omission rate, predicted area, three variations of a jackknife, percent contribution/permutation importance, and environmental variable response curves. The first three directly address overall model performance, while the others attempt to determine both the overall contribution of each environmental variable and the impact that variable values have on the probability of suitable habitat.

In the application of maximum entropy to species distribution modeling, the area under the curve (AUC; values range from 0 to 1) is often used as a comparative benchmark between competing models of the same system. However, the AUC can also be used to measure whether an individual model performed better than random prediction (i.e., an AUC value greater than 0.5). Because the goals of the present study were not comparative in nature, only the latter use of the AUC is relevant.
To create an omission rate curve, the percentage of excluded sample points is graphed against the cumulative threshold, which can be interpreted as the percentage of sample points that should theoretically have a lower predicted probability of suitable habitat. A curve that does not closely mirror the predicted omission rate signifies strong spatial auto-correlation, thereby suggesting that the results of the model should be interpreted with caution. Similarly, Maxent calculates a comparable omission rate for all of the random background points (‘predicted area’). For purposes of comparison, both the sample point omission rate and the predicted area are displayed on a single graph. The predicted area is calculated as a percentage of inclusion rather than exclusion (i.e., a percentage of the background points will have a value that is greater than or equal to a given cumulative threshold). For the present study, the predicted area can be thought of as the percentage of background points that offer a favorable habitat.

Maxent performs three slight variations of a jackknife (once each using AUC, training gain, and test gain as the base metric) as a way of quantifying the importance of each environmental variable. Because all three variations produced very similar results in the current study, only the AUC jackknife will be discussed. To perform the jackknife, the AUC was calculated when (1) only the respective variable was included in the model and (2) the respective variable was excluded from the model. The jackknife output allows for a visual comparison of the predictive power of each variable.

Maxent calculates two more measures of variable importance: percent contribution and permutation importance. Percent contribution is calculated while the model is being
created. For each variable, a coefficient is calculated that relates the change in probability to the change in variable value. The change in training gain (an additional measure of randomness) attributed to each variable is percentage-normalized and termed the percent contribution. However, it should be noted that the percent contribution is unique to Maxent’s calculation of variable coefficients. If another method were used to calculate the variable coefficients, it is plausible to calculate identical coefficients but different percent contributions (Phillips 2006). Therefore, the percent contribution of each variable should be compared against its respective permutation importance and jackknife values.

Alternatively, permutation importance is a measure that is based on the variable value, not coefficient, and is calculated after the model has been finalized. The value of each variable is randomly fluctuated, and the resulting change in the AUC of the model is converted to a percentage, resulting in a variable’s permutation importance. Because the measure is based on the final model, it is, theoretically, a uniform calculation, meaning that regardless of the path by which the model was created, identical values should be assigned.

Finally, for each variable, two response curves are produced, one in which the logistic probability of presence/absence is plotted against potential values of a variable, given that the values of all other variables are maintained at their respective average (joint response curve), and another in which the logistic probability of presence/absence is plotted against potential values of a variable, given that no other variables are included (individual response curve). The joint response curves provide a means to visualize the
most ‘conducive’ values of each variable, given the presence of all other variables, while
the individual response curves permit an examination of the distribution of the
environmental data.

**Results**

In the present study, the species distribution model can confidently be classified as not random (AUC=0.925; Fig. 1). In other words, the environmental data associated with the sample points is non-random, and, given the environmental variables included in the present study, the probability of suitable habitat for *B. occidentalis* in any given location within the state of Oregon can be successfully predicted more frequently than random prediction (Elith et al. 2011). Therefore, the model can be further analyzed to measure the impact that land-use change from 1992 to 2006 has had on the amount of suitable habitat for *B. occidentalis* in the state of Oregon.

Overall, the state of Oregon experienced significant land-use changes from 1992 to 2006 (compare Images 1 & 2). The area of land classified as open-med and shrub-grass increased by 2% and 8%, respectively, while forest and past-crop decreased by 8% and 1%, respectively. Notably, the northeast corner experienced an increase in the density of forest plots, while the forest plots in the western, more-urban half of the state are sparser.

The average omission rate associated with the sample points closely resembles the predicted omission rate (Fig. 2). This suggests that significant spatial auto-correlation is
not present among the environmental data of the sample points (Phillips 2006). If the environmental data were spatially auto-correlated, projection and interpretation of the model would be suspect. Additionally, the predicted area curve follows an exponential decay when graphed against the cumulative threshold, which suggests that many background points offer poor to average habitat, while few background points offer exceptional habitat (Fig. 2) (Phillips 2006).

The AUC jackknife of environmental variables calculated that the distance to open-med and the distance to forest are much more important than the distance to past-crop and the distance to shrub-grass (Fig. 3). Notably, the distance to open-med is the only variable, including all bioclimatic variables, to severely reduce the model’s predictive power when it is excluded. Therefore, it can be argued that the distance to open-med is the most important variable of the present study (Phillips 2006; Buermann et al. 2008).

In line with the results of the AUC jackknife, Maxent calculated the percent contribution of the distance to open-med to be 23.6%, forest to be 13.4%, past-crop to be 5.6%, and shrub-grass to be 0.1%. Likewise, Maxent calculated the permutation importance of the distance to open-med to be 27.1%, forest to be 29.5%, past-crop to be 3%, and shrub-grass to be 0.1% (Table 2).

The joint response curves of the land-use variables demonstrate that as the distance to forest and open-med increases, the logistic probability of suitable habitat significantly decreases (Figs. 4 & 5). On the other hand, change in the distance to shrub-grass appears
to have no impact on habitat suitability (Fig. 6), and the distance to past-crop has a positive relationship with habitat suitability (Fig. 7).

The individual response curves show that the data associated with the distances to forest, open-med, and shrub-grass all follow an exponential decay (Figs 8, 9, & 10, respectively). The relationship between the logistic output and the distance to past-crop is complex, suggesting the presence of threshold and hinge features. Between 0m and 6000m, the relationship is negative; however, beyond 6000m, the relationship is positive (Fig. 11).

Ultimately, when the first 5 km is considered (i.e., the ecologically relevant distance for *Bombus* spp. based on reported flight distance; Walther-Hellwig and Frankl 2000), the individual response curves demonstrate that all land-use categories were generally present within 5 km of sample points. The joint response curves, on the other hand, suggest that when all environmental variables are considered together, proximate plots of forest and open-med, and distant plots of past-crop, provide the most ecologically suitable habitat, while the distance to shrub-grass cannot be used to confidently predict habitat suitability.

Overall, when imported into ArcGIS 10.1 for comparison between 1992 and 2006, the present model predicted that the area of suitable habitat in Oregon increased from 25,210.1 km² to 40,867.7 km², which represents an absolute increase of 6% in suitable habitat area for *B. occidentalis* (Table 3).
Discussion

In the present study, land-use change from 1992 to 2006 in the state of Oregon nearly doubled the total area of suitable habitat for *B. occidentalis* (25210.1 km$^2$ to 40,867.7 km$^2$; compare Images 3 and 4). By that measure, it can be stated that, while a decline of *B. occidentalis* has been documented in the state of Oregon (Cameron et al., 2010), land-use change has not directly acted as a driving force.

Interestingly, the increase in suitable area appears to be closely tied to an expansion of open-med. While this may seem to contradict studies that show a strong connection between local pollinator communities and surrounding natural habitat, the present study may be reconciled with previous findings by considering the general assumptions of the current Maxent model (i.e., probabilities were calculated by using the distance to land-use plots, not the density of land-use plots) and the fact that the present study examined the impact of land-use change across the entire state of Oregon, not at a local scale. Also, the current study demonstrated that joint proximity of open-med and forest was most important. Where the two land-use categories merge has been termed ‘edge’ habitat, and bumble bees have been shown to preferentially choose it for nesting (Svensson et al. 2000).

By comparing the projections of probable distributions, a few locations stand out as significantly different between 1992 and 2006. Most noticeably, the southwest quarter of Oregon is much more favorable for *B. occidentalis* in 2006 than in 1992. The original
land-use maps indicate there has been a significant decline in forested plots (presumably from significant logging in the area surrounding Crater Lake National Park). Many of the forested plots have been converted to shrub and grassland, but roads and other ‘developed’ plots have also noticeably increased in the area. As a result, disturbed areas have increased, and the distance to open-med (i.e., potential floral resources) has decreased. Because the area was still largely forested in 2006, the distance to forest has remained very low. Inadvertently, human activity has increased the probability of suitable *B. occidentalis* habitat from 1992 to 2006 around Crater Lake National Park by way of decreasing the distance between nesting habitat and floral resources.

Examination of the northeast quarter of Oregon reveals that while the area has experienced an overall increase in the probability of suitable habitat due to land-use changes similar to those in the southwest, there are some corridors that have become less suitable from 1992 to 2006. In such corridors, the original land-use maps reveal a noticeable increase in the number and size of forest plots. Because the interiors of larger forests are noticeably more distant from open-med, the necessary combination of nesting habitat and floral resources is perhaps not as readily available, and the overall probability of suitable habitat has decreased.

By considering the above examples, it becomes clear that there must be upper thresholds of both development and forested land beyond which populations of bumble bees are negatively impacted. If development becomes too dense, both nesting habitat and floral resources should decline, and the distance between the two may become insurmountable
for populations of bumble bees (i.e., too many man-made surfaces prevent the presence of both necessary resources; Ahrne et al. 2009). Similarly, while very large, undisturbed forest plots provide necessary nesting habitat, the distance between a large forest’s interior nesting habitat and any surrounding floral resources may be too great to sustain local populations of *Bombus* spp. (Svensson et al. 2000). Therefore, the probability of finding suitable habitat should, theoretically, be highest when both forest and open, disturbed areas are in close proximity.

If all Maxent measures of environmental variable importance are considered jointly with the two aforementioned land-use changes in Oregon from 1992 to 2006, a working consensus can be developed for the present study. The distance to open-med and the distance to forest are, respectively, the two most important land-use categories; as the distance to each habitat increases, the probability of suitable habitat noticeably decreases. On the other hand, the distance to past-crop and the distance to shrub-grass do not significantly contribute to the current model. If either variable (past-crop or shrub-grass) were used to calculate the probability of habitat suitability, correct predictions would occur no more frequently than if the predictions were made at random.

While the distance to forest and the distance to open-med have very similar jackknife values, percentages of contribution, permutation importance values, and individual response curves, the maximum probabilities found in their joint response curves differ markedly. Both demonstrate decaying exponential relationships with the probability of suitable habitat, but the distance to open-med has a maximum probability above 0.9,
while the distance to forest has a maximum probability slightly below 0.6. This divergence suggests that while the distance to forest contributes to the construction of the model, the distance to open-med more significantly contributes to determining the suitability of a given location. Therefore, there must be some underlying ecological characteristic that differentiates the two variables such that the distance to open-med more powerfully predicts suitable habitat than the distance to forest.

The distance to open-med most significantly contributes to the creation of the model and the calculation of suitable habitat; close proximity (< 1 km) is associated with a very high probability of suitable habitat. While this may seem counterintuitive, the relationship may stem from the fact that disturbed areas often experience bursts of floral resources that may contribute to an increased presence and density of pollinators (Romey et al. 2007). Likewise, the edge habitat that often surrounds open-med may potentially offer sufficient nesting grounds (Svensson et al. 2000). Considered together, it may be that the open-med habitat is sufficiently balanced in such a way to offer both the necessary floral resources and the undisturbed nesting habitat.

Concerning the distance to forest, previous studies have demonstrated that the distance to natural habitat significantly predicts the presence of Bombus spp. (Kremen et al. 2004). In the present study, then, it can be extrapolated that the strong relationship between the probability of suitable habitat and the distance to forest directly demonstrates the use of forest by B. occidentalis for nesting grounds (Svensson et al. 2000). The joint response curve of the distance to forest demonstrates that from 0 - 5 km, suitability drastically
drops; to maintain a probability of suitable habitat above the ‘minimum training presence’ (0.1764), the distance to forest should be no greater than 5 km. As previously mentioned, that distance corresponds well to the proposed maximum flight distance of bumble bees. However, the distance to forest does not predict the presence of *B. occidentalis* as strongly as the distance to open-med, and that may be due to the fact that, alone, forest only provides one of the two necessary habitat requirements for bumble bees. While exterior sections of forests may be adjacent to floral resources, interior sections may be too distant from floral resources to support populations of bumble bees.

The significant contribution of bumble bees to agricultural systems cannot be overstated. However, while at first glance the habitat may seem very well suited for bumble bees, many studies have suggested, conversely, that ‘conventional’ agricultural plots detrimentally impact local pollinator populations (Morandin and Winston 2005; Holzschuh et al. 2007; Grixti et al. 2009; Williams and Osborne 2009). Because less than 0.1% of agricultural land in Oregon is farmed organically (USDA 2009), it is safe to assume that *B. occidentalis* is most frequently interacting with ‘conventional’ plots. Additionally, over 75% of the crops grown in the state of Oregon are wind-pollinated plants; wheat, non-alfalfa hay, ryegrass, and corn are a few examples (USDA 2009). Because wind-pollinated plants do not offer optimal nutritional resources for bumble bees, it follows that crop-land does not necessarily predict for suitable habitat.

As measured by jackknife, permutation importance, and percent contribution, the distance to past-crop does not contribute to the predictive power of the model. While its
joint response curve demonstrates a positive relationship between the distance to past-crop and the probability of suitable habitat, all other measures of variable importance suggest little to no variable significance. Similarly, all measures, including its joint response curve, demonstrate that the distance to shrub-grass is insignificant and contributes minimally to the model. Therefore, both the distance to past-crop and the distance to shrub-grass cannot be used to accurately predict habitat suitability.

Proximity to natural habitat (forest) and disturbed areas that may offer floral resources (open-med) most significantly contributed to the calculation of suitable habitat for *B. occidentalis*. Therefore, if the maintenance or introduction of local populations of *B. occidentalis* is desired, the distance to these two variables should inform and direct relevant conservation efforts. According to the present study, the most suitable locations for *B. occidentalis* are areas in which the distance to open-med is less than 1km and the distance to forest is less than 5km. If these guidelines are implemented over a large area, it may be possible to either maintain local populations of *B. occidentalis* or foster their reintroduction via suitable habitat corridors.

Importantly, the present study demonstrated that land-use change may not be a driving force of the noted decline in *B. occidentalis*. That being said, indirect consequences of land-use change may promote other mechanisms of decline. For example, isolation due to large-scale habitat fragmentation may potentially lead to inbreeding depression (Cameron et al. 2011) and, as a result, decreased population sizes and increased susceptibility to pesticide exposure and parasitism (Goulson et al. 2008). Therefore, while land-use
change may not have directly caused the decline, the spatial configuration of land-use change may have facilitated the decline via indirect stresses to local populations.

Qualifications and Limitations

While Maxent provides a statistically sound method for creating a species distribution model with presence-only data, many qualifications do exist that should be addressed. Some concerns arise from the model itself, while other concerns relate to the data used in the present study.

Given the manner in which Maxent functions, various biotic interactions (i.e., plant-animal interactions) are inherently not included, and while the current analysis does specifically account for surrounding land-use (included as continuous data), due to time and resource constraints, the model does not evaluate species-species interactions. In other words, the model does not focus on the presence of a single plant species, rather it lumps ‘meaningful’ land types into 4 categories: forest, open-med, past-crop, and shrub-grass. Even if these four categories do sufficiently summarize the potential environments encountered by *B. occidentalis*, the method inherently introduces the assumption that all sub-categories equally contribute to habitat suitability.

Due to the manner in which samples are often collected, it is always possible that sampling bias exists (i.e., locations ‘expected’ to have bumble bees may be preferentially sampled, or vice versa). However, in the present study, samples originated across a large
geographical area, and the corresponding omission rate demonstrates little spatial auto-correlation. Similarly, because a subset of sample points had to be selected that corresponded to the land-use data (otherwise, the associated data would not properly represent the surrounding landscape), it is possible that the data does not sufficiently represent *B. occidentalis*.

An additional qualification of the current study concerns the assumption that all plot sizes are treated equally with regards to their impact on suitable habitat. Such an assumption means that Maxent treats a single pixel of forest (30m x 30m) and a larger plot (e.g., 100m x 100m) equally. Ecologically, smaller plots may not provide the necessary resources to be of use to *B. occidentalis*, but because no threshold was set to exclude ‘small’ plots of each land-use category, the closest land-use plot to any given sample or background point may be a single pixel. In other words, although converting the categorical rasters to a continuous measurement of distance may better represent the immediate environment, a potential step that may further increase the ability of Maxent to measure the immediate environment would be the determination and implementation of minimum inclusion thresholds for each land-use category.

Finally, Maxent provides no means by which the underlying relationship between a given environmental variable and habitat suitability can be determined; the program only offers quantitative measures that determine the overall importance of each. Therefore, extrapolation via natural history must be used to assign ecological significance to any
meaningful relationships. Certainly, this process must be qualified as inherently biased and limited.

**Future Directions**

Based on the current study, and all associated qualifications and limitations, some potential future directions may provide better insight into the impact that surrounding land-use has on the probability of suitable habitat for *B. occidentalis*.

Specifically, because the land-use categories were grouped together in the present study, it was not possible to determine if any relationships existed between individual crop species and the suitability of a location. However, by breaking down past-crop into various sub-categories, it may be possible to test and quantify the impact that various agricultural systems have on suitability. Sub-categories may be done by crop species, agricultural system (conventional vs. organic), or a combination of the two. As has been suggested, bees are beneficial for crops, but, if the system is harmful to the colony, crops may not be beneficial to bees.

Likewise, the current study created a single group for all ‘usable’ (i.e., not 100% paved) urban plots. Because the category was demonstrated to most significantly impact the probability of suitable habitat, and to better understand the relationship between human disturbance and bumble bees, it is advisable to break this category into its constituents: open space, low-intensity development, and medium-intensity development. As
previously mentioned, too much development is likely very detrimental to local *B. occidentalis* populations.

**Conclusion**

In 2010, Cameron et al. demonstrated that many once-prominent North American bumble bee species (*Bombus* spp.) had experienced significant population declines. Various potential causes were put forth by researchers, including land-use change and habitat fragmentation. The current study combined GIS and SDM to measure the impact that land-use change has potentially had on populations of *B. occidentalis* in the state of Oregon. To do so, realized niche projections for 1992 and 2006 were created in Maxent and compared in ArcGIS 10.1. Contrary to expected findings, land-use change did not directly contribute to the noted decline in Oregon. Conversely, the expansion of open to medium development in once-forested areas increased the area of the habitat most commonly associated with *B. occidentalis* (i.e., ‘edge’ habitat). Therefore, the current study demonstrated that the direct impact of land-use change is not the driving force behind the population decline of *B. occidentalis*; other factors (e.g., neonicotinoids, *Nosema bombi*, indirect effects of habitat fragmentation, and climate change) may prove to more significantly impact bumble bee populations.
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Figures

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Figure 3
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Figure 5
Figure 6
Figure 7
Figure 8
Figure 9
Response of occidentalis to shrubgra

Figure 10
Figure 11
Tables

<table>
<thead>
<tr>
<th>Bio1</th>
<th>Annual Mean Temperature</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bio2</td>
<td>Diurnal Range (Mean of monthly (max temp – min temp))</td>
</tr>
<tr>
<td>Bio3</td>
<td>Isothermality (P2/P7)*(100)</td>
</tr>
<tr>
<td>Bio4</td>
<td>Temperature Seasonality (standard deviation*100)</td>
</tr>
<tr>
<td>Bio5</td>
<td>Max Temperature of Warmest Month</td>
</tr>
<tr>
<td>Bio6</td>
<td>Min Temperature of Coldest Month</td>
</tr>
<tr>
<td>Bio8</td>
<td>Mean Temperature of Wettest Quarter</td>
</tr>
<tr>
<td>Bio9</td>
<td>Mean Temperature of Driest Quarter</td>
</tr>
<tr>
<td>Bio12</td>
<td>Annual Precipitation</td>
</tr>
<tr>
<td>Bio14</td>
<td>Precipitation of Driest Month</td>
</tr>
<tr>
<td>Bio15</td>
<td>Precipitation of Seasonality (Coefficient of Variation)</td>
</tr>
<tr>
<td>Bio18</td>
<td>Precipitation of Warmest Quarter</td>
</tr>
</tbody>
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Table 1
<table>
<thead>
<tr>
<th>Variable</th>
<th>Percent contribution</th>
<th>Permutation importance</th>
</tr>
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<tbody>
<tr>
<td>openmed</td>
<td>23.6</td>
<td>27.1</td>
</tr>
<tr>
<td>forest</td>
<td>13.4</td>
<td>29.5</td>
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<tr>
<td>bio_8</td>
<td>10.2</td>
<td>3.5</td>
</tr>
<tr>
<td>bio_15</td>
<td>9.2</td>
<td>5.2</td>
</tr>
<tr>
<td>bio_12</td>
<td>9.2</td>
<td>15.6</td>
</tr>
<tr>
<td>bio_18</td>
<td>8.7</td>
<td>8.1</td>
</tr>
<tr>
<td>bio_4</td>
<td>7.4</td>
<td>2.1</td>
</tr>
<tr>
<td>pastcrop</td>
<td>5.6</td>
<td>3</td>
</tr>
<tr>
<td>bio_14</td>
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<td>1</td>
</tr>
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<td>bio_6</td>
<td>3.6</td>
<td>2.3</td>
</tr>
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<td>bio_9</td>
<td>3.6</td>
<td>2.6</td>
</tr>
<tr>
<td>bio_2</td>
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<td>0</td>
</tr>
<tr>
<td>bio_1</td>
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<td>0</td>
</tr>
<tr>
<td>shrubgra</td>
<td>0.1</td>
<td>0.1</td>
</tr>
<tr>
<td>bio_3</td>
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<td>0</td>
</tr>
<tr>
<td>bio_5</td>
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Table 2
<table>
<thead>
<tr>
<th>Oregon Total Area</th>
<th>2006 Suitable Area</th>
<th>% of OR</th>
<th>1992 Suitable Area</th>
<th>% of OR</th>
<th>Absolute Change</th>
</tr>
</thead>
<tbody>
<tr>
<td>251420.7</td>
<td>40867.7</td>
<td>16%</td>
<td>25210.1</td>
<td>10%</td>
<td>6%</td>
</tr>
</tbody>
</table>

Table 3
Images

Image 1
Image 4
Appendix

Maxent Model Parameters:

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Setting</th>
</tr>
</thead>
<tbody>
<tr>
<td>Regularization</td>
<td>3</td>
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<tr>
<td>20% Subsample</td>
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</tr>
<tr>
<td>Seed</td>
<td></td>
</tr>
<tr>
<td>50 replicates</td>
<td></td>
</tr>
<tr>
<td>5000 iterations</td>
<td></td>
</tr>
<tr>
<td>All others default</td>
<td></td>
</tr>
</tbody>
</table>
Land-use Categories (MRLC.gov):

<table>
<thead>
<tr>
<th><strong>Forest: Deciduous, Evergreen, and Mixed Forest</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td>Deciduous Forest = areas dominated by trees generally greater than 5 meters tall, and greater than 20% of total vegetation cover. More than 75% of the tree species shed foliage simultaneously in response to seasonal change.</td>
</tr>
<tr>
<td>Evergreen Forest = areas dominated by trees generally greater than 5 meters tall, and greater than 20% of total vegetation cover. More than 75% of the tree species maintain their leaves all year. Canopy is never without green foliage.</td>
</tr>
<tr>
<td>Mixed Forest = areas dominated by trees generally greater than 5 meters tall, and greater than 20% of total vegetation cover. Neither deciduous nor evergreen species are greater than 75% of total tree cover.</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th><strong>Open-Med: Open Space to Medium-Intensity Development</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td>Open Development = areas with a mixture of some constructed materials, but mostly vegetation in the form of lawn grasses. Impervious surfaces account for less than 20% of total cover. These areas most commonly include large-lot single-family housing units, parks, golf courses, and vegetation planted in developed settings for recreation, erosion control, or aesthetic purposes.</td>
</tr>
<tr>
<td>Low-Intensity = areas with a mixture of constructed materials and vegetation. Impervious surfaces account for 20% to 49% percent of total cover. These areas most commonly include single-family housing units.</td>
</tr>
<tr>
<td>Medium-Intensity = areas with a mixture of constructed materials and vegetation. Impervious surfaces account for 50% to 79% of the total cover. These areas most commonly include single-family housing units.</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th><strong>Past-Crop: Pasture/Hay and Cultivated Crops</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td>Pasture/Hay = areas of grasses, legumes, or grass-legume mixtures planted for livestock grazing or the production of seed or hay crops, typically on a perennial cycle. Pasture/hay vegetation accounts for greater than 20% of total vegetation.</td>
</tr>
<tr>
<td>Cultivated Crops = areas used for the production of annual crops, such as corn, soybeans, vegetables, tobacco, and cotton, and also perennial woody crops such as orchards and vineyards. Crop vegetation accounts for greater than 20% of total vegetation. This class also includes all land being actively tilled.</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th><strong>Shrub-Grass: Shrub/Scrub and Grassland/Herbaceous</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td>Shrub/Scrub = areas dominated by shrubs; less than 5 meters tall with shrub canopy typically greater than 20% of total vegetation. This class includes true shrubs, young trees in an early successional stage or trees stunted from environmental conditions.</td>
</tr>
<tr>
<td>Grassland/Herbaceous = areas dominated by graminoid or herbaceous vegetation, generally greater than 80% of total vegetation. These areas are not subject to intensive management such as tilling, but can be utilized for grazing.</td>
</tr>
</tbody>
</table>