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ECOLOGICAL FUNCTIONS AND CONSEQUENCES OF
CRANBERRY (*VACCINIUM MACROCARPON*) AGRICULTURE IN
THE PINELANDS OF NEW JERSEY

by

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ABSTRACT OF THE DISSERTATION

Ecological functions and consequences of cranberry (*Vaccinium macrocarpon*) agriculture in the Pinelands of New Jersey

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This dissertation examined the immediate and long-term ecological influences of cranberry farming on the surrounding fauna and flora.

The first chapter presents a field study examining anuran usage of water bodies within active and newly abandoned cranberry farms. Overall, anuran species exhibited varied preferences for habitats based on their different hydrological requirements. *Rana clamitans* and *Bufo woodhousii fowleri* showed higher density in active than abandoned farms, probably due to different levels of predation. *R. clamitans* also showed a prolonged breeding period in active farms, coinciding with the more stable water level managed by irrigation. *R. virgatipes* and *R. sphenoccephala* preferred abandoned farms, probably because their overwinter and breeding behavior coincided with intensive farming activities. This chapter demonstrated that anurans selectively utilize diverse water bodies within cranberry farms and human cultivation activities can positively or negatively influence their survival.

In the second chapter, I conducted two greenhouse experiments to examine cranberry farming's short-term legacy effect on the seed bank composition and

germination in newly abandoned cranberry farms. The first experiment showed that the human modified post-agricultural edaphic conditions, including soil hydrology and soil depth, were the major factors affecting the seed bank viability, composition and density of germinated plants. For restoration purposes, flooding can increase germination density but does not affect species composition. The second experiment showed that weed colonies and cranberry remnant prevented seed bank germination. This chapter demonstrated the legacy effect from cranberry cultivation on the initial stage of succession.

The last chapter examined cranberry farming's long-term legacy on the structural development of vegetation and the composition of anuran communities. Even after half a century, the vegetation's coverage and mean height still exhibited linear changes along the bog sequence in cranberry farms, coinciding with the gradual hydrological changes in bog units from upstream to downstream. The densities of anuran species that prefer permanent waters were negatively correlated with vegetation coverage and height. However, model selection showed vegetation or anuran variables did not exhibit clear variation among farms, despite decades-long differences in their ages since abandonment. This result indicated agriculture's legacy effect during later succession was not mitigated by time.

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INTRODUCTION

The work in this dissertation describes the role of anthropogenic and natural processes in an agricultural system. The relationship between agriculture and the surrounding environment has existed and developed throughout human history, and now the recent industrialization of farming practices raises concerns and questions about the direction of agriculture's future development. These recent agricultural developments over-emphasized the anthropogenic function of agriculture, while ignoring the ecological consequences of agricultural practices. We need to enact more proper agricultural schemes in order to halt and reverse these negative impacts. To achieve this goal, we first have to understand the connection between each specific agricultural system and its surrounding ecosystems.

In this dissertation, I first evaluated the ecological function of active cranberry farms and their effects on the associated fauna and flora in the Pinelands region of New Jersey. Secondly, I examined the lingering influences of agriculture on the initial stage of succession after cultivation was terminated. I further traced the dynamics of fauna and flora within the farms decades after abandonment to depict the persistent legacy effects of farming and their consequences on the long-term re-colonization of the natural communities.

Agriculture's ecological functions:

The practice of farming began before recorded human history. Farming freed humans from continuous searching for food, and allowed us to develop other aspects of higher civilization. Farming is the essential link between human civilization and our innate nature as an animal predator. Thus, it is ironic that the current, more "civilized"

farming techniques have put us at odds with nature. The industrialized, mechanized and chemical catalyzed agriculture has serious consequences on the future of our environment (Kimbrell 2002). The most worrisome consequences of modern agriculture are loss of genetic diversity (Ehrenfeld 2009), species extinction (Green et al. 2005), loss of natural habitats, eutrophication and greenhouse gas release (Tilman et al. 2001). Even the future of agriculture itself is blurred by the immense amount of soil degradation and chemical contamination that is happening globally (Kirschenmann 2003).

People have started to look for alternatives. The organic movement was proposed in the early 20th century to as a way to reduce agriculture's reliance on synthesized chemicals. However, the practice of organic farming is not always feasible for farmers because of economic or practical reasons. The more recent development of agri-environmental schemes aimed to seek more cost-effective methods that can be adopted by more farmers (Defra 2002; McNeely & Scherr 2003; MacDonald *et al.* 2007). These schemes placed emphasis on finding the equilibrium between a farm's productivity, the farmer's economic benefit and the protection of the natural environment (McNeely & Scherr 2003). Farmland is regarded as a component of an ecosystem and it is expected to fulfill a range of ecosystem functions, including the need of farming communities. The ecosystem function can be as local as improvements in downstream water quality, to as large-scale as the regulation of the global carbon cycle (Swinton et al. 2007).

One main ecosystem function of ecoagriculture is to provide wildlife habitat. A large body of literature has been dedicated to seeking landscape components that can accommodate wild animals. It is believed that the various "natural" remnants within the farms have contributed tremendously to supporting wildlife in the farm landscape. The

margins around arable fields (Sparks *et al.* 1996; Le Caur *et al.* 2002; Marshall & Moonen 2002; Vickery *et al.* 2009) are critical to the avian communities. The remaining woodlots and wetlands within farmlands benefit the survival of amphibians (Knutson *et al.* 2004; Weyrauch & Grubb 2004) and birds (Cunningham *et al.* 2008; Haslem and Bennett 2008). As a result, many studies are conducted on how to increase the proportion of “natural” habitats and to improve their habitat function without interfering with agricultural activities (Harvey *et al.* 2005; MacDonald *et al.* 2007). On the other hand, the cultivation areas (i.e. fields in cropland) and their adjacent areas (i.e. irrigation ditches) are often simply considered to be of low ecological value (Freemark & Kirk 2001; Pywell *et al.* 2005). Except as a source of crop residue and invertebrate animals that serve as prey, the cultivation areas are rarely regarded as valuable for wildlife, if not regarded as antagonistic to wildlife. The few studies that examined wildlife activities in actively-cultivated areas were conducted during winter or fallow seasons (Bird *et al.* 2000; Elphick 1998, 2004; except Maeda 2005).

It is not difficult to understand why these components of a farmland are valued less as wildlife habitats when compared to the natural elements. Human farming activities unavoidably change the physical structure of these habitats and bring chemical contamination into water and soils. This kind of disturbance is commonly considered to be harmful for wildlife (Hamer *et al.* 2004; Griffis-Kyle & Ritchie 2007). However, we should not assume the negative impact is unavoidable. Human impacts on different trophic levels of flora and fauna can create complicated interactions, which can benefit certain animal or plant communities (Morin 1984; Boone *et al.* 2007). Human activities can also stabilize the habitat conditions in these farmland components, in comparison to

natural habitats that are subjected to severe natural weather conditions, e.g. drought or flooding (Pyke & Marty 2005). In a farmland habitat, these potential complex interactions demand in-depth studies to develop a comprehensive understanding of wildlife's reaction to human activities.

The cranberry farm system, the targeted study system of this dissertation, contains both relatively natural habitats (such as the reservoir) as well as intensively cultivated areas (cultivation beds and irrigation ditches). Compared with many types of upland farms where the landscape is relatively homogeneous, the diverse habitats within cranberry farms create high within-farm heterogeneity that is subjected to various levels of human disturbance. In the first chapter of this dissertation, I examined the wildlife habitat function of cranberry farms and evaluated how the mosaic wetland habitats (both natural and anthropogenic) contribute to the ecosystem function of cranberry farms. By comparing the distribution of anurans between active and abandoned farms, I further depicted how human activities contribute to or impact the habitat functions of cranberry farms. This chapter demonstrated the immediate ecological values and impacts of active cranberry farming on the Pine Barrens ecosystem.

Legacy: farmland's effect along time

The immediate ecological function of active farmlands is only a fraction of the whole picture regarding the effects of farmland on ecosystem function. Farmland construction can permanently change the topology of the landscape; continuous irrigation can alter the underlying water table; the chemical and physical disturbances can change the texture and chemical features of soils. These effects can last decades or even centuries after human activities cease (Harmer et al. 2001). Without addressing these long-term

legacy effects, we cannot complete the image of a farmland's ecological functions and consequences.

Agriculture's legacy effect can often be clearly evident. The remnant plant tissues create barriers to the re-colonization of natural plant communities (Ferguson *et al.* 2003). Similarly, the clearance of original vegetation within an agriculture landscape eliminates propagule sources for vegetation regeneration (Hooper *et al.* 2004). Despite these conspicuous effects, many long-term impacts can be concealed, while the interaction among these factors will further complicate the post-agriculture community dynamics. A large number of possible interactions have been observed in post-abandonment farmlands. Changes of soil physical and chemical properties (Herrera & Finegan 1997; Knops & Tilman 2000) and changes in seed bank composition can affect the initial re-colonization of herbaceous species (Guariguata & Ostertag 2001), which can allow the invasion of exotic species (Hooper *et al.* 2004). Inter- and intra- specific competition among exotic and native species alters the pace of biomass accumulation (Myster & Pickett 1990), and consequently affects the rates of species accumulation and the ultimate species composition in the secondary succession. Guariguata and Ostertag (2001) reviewed the factors that influence secondary succession in abandoned farmlands. They concluded that secondary succession is largely dependant on site-specific and land-use specific factors which cannot be predicted based on observation in other superficially similar systems.

In the interest of achieving a comprehensive understanding of cranberry cultivation's long-term ecological consequences, I conducted further research to examine the factors that affect plant and animal succession in the abandoned cranberry farms. I predicted that the succession in abandoned cranberry fields greatly diverges from our knowledge of

old-field succession because cranberry is a wetland crop. Succession in natural wetlands differs significantly from succession in upland habitats. In spite of their similar reliance on propagule availability (van der Valk & Davis 1978; Foster 2001), wetland succession is largely driven by the hydrological condition within the habitat in a variety of wetland systems (van der Valk 1981; 2005), while in upland succession there is not such a universal driving factor.

Studies of secondary succession in wetland farms are rare when compared with the abundance of literature dealing with old-field succession in upland habitat, even though rice, as another prominent wetland crop, covers large earth areas worldwide. Most of the few available studies were conducted with a restoration perspective to observe the post-restoration fauna and flora dynamics. Lee *et al.* (2002) used a space-for-time approach to show that in abandoned rice fields, as soil moisture decreased during post-agriculture succession, plant communities went through a vegetation sere from herbaceous to alder communities. Another study (Comin *et al.* 2001) showed the high efficiency of water N and P removal in abandoned lowland rice paddies; they also demonstrated that avian communities prefer intermediate plant cover in abandoned rice paddies. Lu *et al.* (2007) exhibited the increased N and P in organic soil during after-restoration succession in rice fields. Only one previous study (Yamada *et al.* 2007) looked specifically at the effect of agricultural practice on succession, and they reported that 1-year fallow practice can increase the diversity of paddy plants during restoration.

Hence, in order to understand cranberry cultivation's effect on post-agricultural succession, I targeted my first study of agricultural legacies (chapter 2) on the initial plant establishment stage of post-agricultural succession. I examined the seed bank

composition within abandoned cranberry soils to assess the effects of altered hydrology and sanding practices during cranberry production. I also examined the seed bank's viability and their germination response under different flooding regime.

With the knowledge of cranberry production's effect on initial succession, I then sampled the vegetation structure and anuran community at various stages of post-agriculture succession (Chapter 3). Cranberry farms with older designs allowed me to examine altered hydrology's effect on vegetation structure development and anuran community composition, in addition to examining the vegetation structure and anuran species' change as time passed after the cessation of human activities. Results of these studies demonstrated the ecological consequences of wetland agriculture in the unique Pine Barrens' wetland system.

Cranberry: a special wetland plant

In this dissertation, agriculture's ecological function was studied within the cranberry farm system. Cranberry (*Vaccinium macrocarpon*) is an indigenous freshwater plant thriving on the acidic peat soil of the Pine Barrens of New Jersey. It grows in the cool, moist, boggy regions of the Pine Barrens and can be found around the margins of lakes, in bogs and along stream banks (Eck 1990). It has been cultivated locally for more than 150 years. Many present cranberry farms in New Jersey are owned by family growers, who have made their living working in these wetlands for generations (Jones 2000). Currently there are 3,100 acres of active and over 8,000 acres of abandoned cranberry farms (Zampella *et al.* 2006), yet there are numerous acres of upland or wetland habitats that are associated with these farms. Cranberry production, like rice production, requires continuous irrigation and flooding to maintain saturated soil.

However, the special features of cranberry make cranberry farms more closely affiliated to the surrounding wetland ecosystem. The close connection between cranberry farms and the Pine Barrens' wetlands makes it an ideal target to achieve the goal of this dissertation. These features of cranberry plant are summarized in this last section of introduction.

Water is a key element for the growth of cranberry crops because cranberry is adapted to the saturated bog environment (Eck 1990). It can adapt to submergence in the wet winter seasons, although in the growing season even partial submergence can create damage to the plants. Over the years of cranberry cultivation, cranberry farmers have developed various usage of water for cranberry growth. The main usages include winter flooding to protect crops from frost damage (December to March); irrigation during the growing season; sprinkler usage in the summer to protect from heat damage; and fall flooding (September or October) to harvest cranberry fruits. In addition, water is also used for sanding (a process to add more sand onto the cultivation surface) as well as disease and insect control (DeMoranville *et al.* 2008). Therefore, cranberry farms are typically constructed along freshwater streams, with natural lakes or dammed streams as their reservoirs. Within each farm, various water-bodies, such as cranberry bogs, irrigation ditches and storm-water drainages are constructed and are connected with ditches to manage the water level to achieve the various functions. Water is eventually fed back to the downstream wetlands.

Due to the importance of water to cranberry growth, the quality of the incoming water is always a major concern of cranberry growers. Chemical contaminations that are likely to increase the water pH can severely change the acidic soil quality within the

cranberry farms and hence reduce their productivity (Hanson & Stein 1999). Even the usage of road salt may be a potential threat to the productivity of cranberry farms (Eck 1990). Furthermore, in 1959, a nationwide scare of herbicide remnant on cranberries historically impaired cranberry production and resulted in an upsurge of cranberry farm abandonment (Jones 2000). This incident made many cranberry growers even more cautious about the usage of agricultural chemicals. Studies have shown that a large proportion of cranberry growers in Massachusetts and New Jersey understand and apply integrated pest management (IPM) as a means to reduce the usage of agricultural chemicals (Jones 2000; Blake et al. 2007). IPM programs do not completely eliminate pesticide application; rather, the usage of pesticide is combined with other control methods and is based on measured pest pressures. These efforts can maximize its control effect and minimize the impact on the environment. Commonly applied strategies include pheromone traps, dropping the water level before spraying (Sandler & DeMoranville 2008), and weed mapping (Oudemans et al. 2002).

In contrast to many other upland or wetland crops, cranberry requires little fertilizer input. About 95% of required nitrogen comes from the decomposition of soil organic matter (Davenport 1993). In fact, excess nitrogen fertilizer can cause various problems for cranberry production, such as overgrowing of vegetative tissues, promoting weed growth, and damaging fruit quality (Eck 1990). The net nitrogen loss in the surface water discharge has been shown to be similar to a surface water dominated freshwater wetland, and much lower than residential development (Howes & Teal 1995). Phosphorus fertilizer application is necessary because cranberry plants cannot take sufficient soil phosphorus during their growing season (Sandler & DeMoranville 2008). However, the

phosphorus fertilizer addition is still substantially lower than for many other crop types because, evolutionarily, cranberry plants are adapted to low nutrient, high acidity soil. Phosphorus content in the water discharge is seasonal, with the highest during the cranberry harvesting season and winter because of the reduced soil oxidation during flooding (Howes & Teal 1995). In general, water discharge from cranberry farms has very low soluble nitrogen and phosphorus (Eck 1990).

While concern for contamination from fertilizer application is low, pesticide application in cranberry farms is considered a major source of environment contamination. Although the IPM practices can potentially reduce the pesticide level in discharged water and reduce pesticide application on non-targeted areas, the impact of pesticide cannot be eliminated and still needs to be critically considered. Chlorinated insecticides and herbicides are believed to persist in cranberry soils because the soils' high acidity and saturation can reduce the survival of microbial communities, consequently reducing the speed of chemical degradation (Eck 1990; Wan *et al.* 1995). Thus, while cranberry agriculture might be expected to have little impact on the environment due to cranberry's adaptation to low nutrient environments, the overall impact of this agricultural system must be critically examined. Together, these unique features of cranberry agriculture make this an excellent system to study the ecological functions and consequences of an agricultural system, and assess the ecosystem services provided by this habitat.

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CHAPTER 1

Anuran's usage of cranberry farms in the Pinelands, New Jersey: evaluation of habitat diversity and human cultivation activities

ABSTRACT

1. The influence of wetland farms on anurans has not been examined as explicitly as has the impact of upland farms. I studied anuran communities within various habitats of cranberry farms. I examined whether different water-bodies within the farms can be utilized by anurans with varied hydrological requirements; and whether human farming activities can change, negatively or positively, the habitat preference of these species.
2. I conducted anuran vocal surveys during their breeding season in both active and newly abandoned (no human activities) cranberry farms. Three habitat types (cranberry bogs, main ditches and reservoirs) within each farm were surveyed for four local Pinelands species. I applied a multinomial model to interpret each species' density from the ranked calling data. For each species, I selected the most parsimonious model to compare its density and occurrence among the three habitats and between farms with and without human activities.
3. Green frogs (*Rana clamitans*) showed high density in the bog habitats of active farms, where they exhibited prolonged calling activities in late summer which coincided with the stable water level managed by irrigation. Fowler's toads (*Bufo woodhousii fowleri*) had high density in the ditches of active farms and the reservoirs of abandoned farms. Both species' high density within active farms might be attributed to cranberry's low fertilizer requirement and the lower predation pressure in active farms.
4. Carpenter frogs (*R. [Lithobates] virgatipes*) exhibited a preference for the reservoir habitat in both farm types. They also had higher density in abandoned farms, which could

be a result of the repeated water fluctuation managed by farmers in the fall. The density of southern leopard frogs (*R. sphenoccephala*) varied to a great degree in all habitats. Water fluctuation and the intensive cultivation activities during early spring may have contributed to their low occurrence in active farms.

5. Synthesis and applications: farmlands with diverse habitats will support higher diversity of anurans. Anurans can benefit from human agricultural activities if those activities help reduce the impact of drought or predation. We need to create diverse habitats within farmlands to fulfill the varied habitat requirements of anurans.

Key-words: anurans, cranberry cultivation, wetland agriculture, farm abandonment, farm habitat diversity, hydrology management, vocal survey, imperfect detection, latent abundance

INTRODUCTION

The loss of natural habitat due to anthropogenic development is believed to be one of the main reasons for the global amphibian decline. (Weyrauch and Grubb 2004; Cushman 2006). Specifically, the construction of farmlands within woodlands or natural wetlands in rural areas has been shown to decrease habitat integrity and accelerate the loss of amphibian diversity. Previous research found that the area of agricultural land is negatively correlated with amphibian occurrence (Knutson et al. 1999; Piha et al. 2007). The impact from agriculture is especially devastating if the farmlands are constructed by draining wetlands and clearing upland forests (Knutson et al. 1999). Not only do these practices destroy amphibian habitats by converting them into inhospitable farms, but the remaining suitable wetland is also fragmented, prohibiting the migration of remnant

amphibians in the region (Cushman 2006).

However, when farmlands are constructed to retain sufficient habitats such as wetlands, woodlots, and remnant forest patches, they can potentially function as refuge habitats for amphibians. The proportion of the remaining wetlands within the farmland, along with their characteristics (e.g. patch size, pH, and hydroperiod) are essential to the farmland's ability to sustain amphibian communities (Baker & Halliday 1999; Knutson et al. 2004; Weyrauch & Grubb 2004; Babbitt 2009). These findings suggest that wetland agriculture, such as rice paddies and cranberry bogs, can potentially function as refuges or corridors for amphibians. They can help buffer human impacts in a landscape where the remaining natural habitats are encroached upon by human residential or commercial development. In many regions of the world, agricultural products from wetland farms are the major food source, and wetland farms occupy a large proportion of land (Yamada et al. 2007; Verhoeven & Setter 2010). However, despite their prevalence in many areas, there are surprisingly few ecological studies conducted to evaluate the ecological function of these farms as amphibian habitat (but see Fujioka & Lane 1997; Dure et al. 2008).

In this study, I examined the habitat value of cranberry farms in the Pinelands of New Jersey. Cranberry (*Vaccinium macrocarpon*) has been cultivated in this region for almost two centuries. The active farms cover about 1250 ha in the central region of the Pinelands National Preserve, while an additional 3200 ha of inactive farms are scattered throughout the region (Zampella et al. 2006). The farms are usually constructed along major roads with close proximity to freshwater streams or lakes which serve as their reservoir. The cultivation of cranberries requires clean freshwater input throughout the year for various functions. During the growing season, the cultivation beds are watered

by sprinklers to protect them from over-heating; in the fall, the beds are flooded for cranberry harvest; in the winter, cultivation beds are submerged to protect the crop from frost damage. In order to bring in water to achieve these functions, a variety of water related structures are constructed in the farm (Fig.1). The cultivation beds (hereafter “bogs”, around 2 ha) are excavated to be lower than the ground and are surrounded with irrigation side ditches (around 2-3m wide). Soil is saturated during the growing season, and occasionally there are patches of standing water on the surface. There are a series of connecting ditches (hereafter “ditches”, around 5-8m wide; 1m deep) in the farms to connect all the bogs to the main water source (hereafter “reservoir”, open water with floating vegetation). The water level in the main ditches and reservoir is managed during the growing season to meet the water requirement of the bogs (e.g. to drain excess water after precipitation or to provide more water during hot weather).

With these structures, cranberry farms provide a variety of habitats with different physical and biological characteristics; this contrasts with many major upland farm types in North America, which create large areas of uniform habitat. This habitat heterogeneity can potentially support different anuran species. Thus, the first focus of this study was to survey and evaluate the various anuran species’ distributions and abundances within the different habitats in the farms (i.e. bogs, ditches and reservoirs). I hypothesized that these habitats would be utilized by different anuran species with various hydrological requirements during their breeding season.

The second focus of this study was to examine whether and how human activities might affect the ecological function of the farms as anuran habitat. Farmlands are generally believed to reduce the amphibian survivorship because of disturbance from

human activities. Farmers regularly mow, spray and irrigate the farms to increase crop productivity, especially during the growing season. It has been shown repeatedly that amphibians are adversely affected by a range of agricultural chemicals (Boone and Semlitsch 2002; Griffis-Kyle and Ritchie 2007), as well as reduced vegetation coverage and increased virus exposure because of human disturbance (Burton *et al.* 2009). However, agricultural activities do not exclusively bring negative impact to the survival of anurans. Pyke and Marty (2005) suggested that cattle grazing can offset the impact of climate change on the vernal pond's hydrological variation, which benefited endangered salamander species. Burton *et al.* (2009) demonstrated that controlled cattle grazing in wetlands may increase post-metamorphic growth and survival of bufonids. Both of these studies suggested that with proper management, livestock grazing can potentially stabilize habitat hydrological conditions and reduce the impact of natural habitat variability (i.e. seasonal flooding or drought).

Likewise, the cultivation of cranberries involves active water management to maintain a suitable water level for the crop's growth, which can create a stable hydrological environment for anurans. Compared with many other crop types, nitrogen fertilizer requirement in cranberry production is minimal (Eck 1990; Sandler & DeMoranville 2008), which reduces the potential impact of nitrogen fertilizers on the amphibian communities (Smith *et al.* 2005). In addition, the lower diversity and density of fish communities in agricultural wetlands due to human activities (Mensing *et al.* 1998) can reduce the predator pressures on anurans. The interaction of these factors can potentially create beneficial effects on anuran communities (Boone *et al.* 2007).

Therefore, the second focus of the study was to examine whether the actively

managed cranberry farms increase or decrease the breeding activities of anuran species. I hypothesized that compared with farms that were abandoned (i.e. where active cultivation has stopped but the farm's infrastructure still remains), active cranberry farms can support higher densities of certain anuran species due to more stable water level and reduced predation. The result of this study can enrich our knowledge of anuran species' response to ongoing agricultural activities via direct or indirect effects. It was expected that this may further help to indicate proper wetland farming strategies.

METHODS

Study Sites:

The anuran survey was conducted in three active (ACT) and three abandoned (ABD) cranberry farms (Table 1) in the Pinelands of New Jersey. The three abandoned farms (ABD1,2,3) were formerly owned and cultivated by the A.R. DeMarco Enterprises from the 1940s until late 1990s. Since then they have become the Franklin Parker Preserve and are no longer cultivated. The farm's infrastructure (dams, dikes and ditches) is maintained by the New Jersey Conservation Foundation, but their hydrology is no longer actively managed for cranberry production as in the active farms. Within each farm, I surveyed multiple locations of three major habitat types: cranberry bog, main irrigation ditch, and the reservoir (Table 1).

Frog calling survey:

Four anuran species were surveyed in this study: carpenter frog *Rana [Lithobates] virgatipes*, southern leopard frog *R. sphenoccephala*, green frog *R. clamitans*, and Fowler's toad *Bufo woodhousii fowleri*. All four species naturally inhabit the Pinelands

within New Jersey. The carpenter frog is considered “restricted” to the Pinelands, while the other three species are considered “wide-spread” in New Jersey (Bunnell and Zampella 2008).

The surveys were conducted between sunset and midnight. Each survey location was visited by walking in order to minimize the effect of human disturbance on anuran calling intensity. The sequence of locations visited within each farm was alternated in order to remove bias caused by the variation of anuran calling intensity at different times of night. I spent five minutes at each survey location, during which, anuran calls were identified and the highest calling intensity of each species was ranked and recorded. The ranking used was: no anuran heard (0); discrete, non-overlapping calls (1); discrete, overlapping calls (2); and chorus (3) (adopted from North American Amphibian Monitoring Program survey protocols, Patuxent Wildlife Research Center).

A preliminary survey was initiated in farm ACT2, ACT3 and ABD1 in year 2006. In year 2007 and 2008, all six sites were surveyed from April to August. The three year survey data was first used to depict the specific chronology of each anuran species in the Pinelands of New Jersey. To do this, I plotted the average calling intensity of each species from each habitat over time (2006, 2007 and 2008). Based on the chronology, the peak months of each species’ chronology was determined (Table 2). Survey data from 2007 and 2008 was then used in the following analysis to compare anuran abundance in different habitats of the two farm types.

Water level measurement:

In order to interpret the correlation between the anuran calling activities and fluctuation of managed water level in late summer, I measured the water level in the three

habitats within active and abandoned farms during an 11 day period (Aug. 16th to 27th, 2008) when there was no precipitation. Within each farm, each habitat type was sampled at three locations with three independent measurements at each location. Because the bog habitat (cultivation beds) covers large areas where the surface water level was hard to measure and average, I measured the water level within the side ditches that surround these cultivation beds. These side ditches provide the water supply for the cultivation beds, and so reflect the water level change in cultivation beds.

Data analysis:

I applied the modeling procedure proposed by Royle and Link (2005) to model the calling index of each species for each habitat (i.e. bog, ditch and reservoir in active and abandoned farms). This method is superior to many traditional statistical interpretations of the calling survey data because it does not hypothetically link the calling indices (0,1,2,3) with the “precise” anuran densities. Rather, it aims to estimate the “maximum potential calling index” for each habitat (i.e. the latent abundance class $N=0, 1, 2, \text{ or } 3$). It uses the observed calling intensities to generate the probability distribution of the maximum calling index for each habitat (i.e. the latent abundance distribution: ψ^k $k=0, 1, 2, 3$ for $N=0, 1, 2$ or 3 ; $\sum \psi^k=1$). It applies integrated likelihood method to find the latent abundance distribution which can maximum the likelihood of the observed data. The mean of the calling intensity for each habitat is then calculated as $\bar{N} = 0 * \psi^0 + 1 * \psi^1 + 2 * \psi^2 + 3 * \psi^3$, and the variance of the mean is estimated using the variance of ψ^k , $k=0, 1, 2, 3$.

Secondly, this method also takes into consideration the imperfect detection at each survey location during an anuran calling survey. For instance, if a survey location's true

calling intensity was $N = 2$, the observed value could be $y = 0, 1$, or 2 . Conventional methods usually do not directly address this issue, but use increased survey frequency to reduce the impact of imperfect detections from single surveys. The method proposed by Royle and Link (2005) specifies six parameters to model the imperfect detectability of each species. Parameters p_1, p_2 and p_3 are the “correct classification” probabilities given the true calling index during a sample was $1, 2$ or 3 , respectively. Parameters $\beta_{21}, \beta_{31}, \beta_{32}$ are the conditional misclassification probabilities (e.g. β_{32} is the probability that the observed calling index $y = 2$ if the true $N = 3$ and $y \leq 2$; See Appendix 1 for details). All six parameters could vary freely in the model, but with prior knowledge, certain parameters can also be constrained to create submodels (e.g. $p_2 = p_3$ means the species could be equally correctly detected when $N = 2$ or $N = 3$). The fit of the submodels is evaluated with the model selection strategy (AIC, as described below). The six detectability parameters are then used to calculate the likelihood of obtaining observed calling intensity data by numerically integrating the likelihood over the latent class distribution (ψ^k $k = 0, 1, 2, 3$). The detectability parameters (the “ p ”s and “ β ”s) and the latent distribution (ψ^k) that can yield the maximum likelihood is reported as the model output. This maximization procedure is conducted by the `nlm` function in the statistical software R (2.9.2).

In my analysis, I modified Royle and Link’s (2005) method to examine whether each species’ latent distribution was affected by the two targeted factors: farm status (active vs. abandoned), habitat types (bogs, ditches and reservoirs), as well as their interactions. I generated a series of candidate models which specified latent distributions for the targeted factors. For instance, if farm status affected the abundance of a species (which meant the species had different abundance distribution in the active and

abandoned farms), the observed calling density would be best fitted by models with two sets of latent distributions ($\psi_{active}^{k=0,1,2,3}, \psi_{abandoned}^{k=0,1,2,3}$). Similarly, if the species had different density distributions in the three habitats, the model would have different latent distribution for each habitat type ($\psi_{bog}^{k=0,1,2,3}, \psi_{ditch}^{k=0,1,2,3}, \psi_{reservoir}^{k=0,1,2,3}$).

I specified five candidate models for each species, with the following combination of latent distributions: 1) farm status; 2) habitat type; 3) farm status and habitat types with no interactions; 4) farm status, habitat type and their interactions; 5) no farm or habitat effect. (See appendix 2 for the detailed candidate models). I applied Akaike Information Criterion (AIC) model selection strategy to obtain the candidate model that best fits the data (Burnham and Anderson 2002). For each candidate model, I also created a set of submodels by changing constraints of the detectability parameters (the “p”s and “β”s). The AIC criterion was also used to choose the best submodel that fitted the observed data. In each model, I applied the same detectability parameters in both farm status and all three habitats, because I assumed that the physical structures of the habitats and the abandonment status of the farm did not change the detectability of anurans.

RESULTS

Without exception, the top model for all four species included latent probability distributions of farm status, habitat types, and their interactions (candidate model #4 in *Data Analysis* and *Appendix 2*). This result demonstrated that the latent abundance of each species varies among all three habitat types and differs between the active and abandoned farms. The interaction term indicated that the variation in the three habitats also differs between active and abandoned farms.

Figs. 2 to 5 present each anuran species' mean calling intensity, which was calculated with the latent abundance distribution (See *Data Analysis*). These calling intensities are indicators of each species' density in the different habitats. If the calling intensity was low, there could be two possible causes: 1) anurans are present at many locations, but the calling intensity was low at all locations; 2) anurans were absent at most locations. In order to examine which of the two reasons caused a low calling intensity, for each species, I also graphed the percentage of locations with no calls detected (i.e. ψ^0 in *Data Analysis*), as shown by graph (b) in Figures 2 to 5.

Green frogs had exceptionally high calling intensity in the bog habitat of active farms, while its densities in all other habitats are relatively comparable (Fig. 2a). Their exceptional preference of this habitat is also demonstrated by their high ratio of presence (Fig.2b). Compared to the bog habitat in abandoned farms where they were absent in $59.2 \pm 3.4\%$ of the survey locations, they were only absent in $2.1 \pm 3.6\%$ of the surveyed bogs in the active farms.

Fowler's toads also exhibited differed habitat selection patterns in active and abandoned farms. In active farms, they had the highest calling activities in the ditches and secondly the bogs (Fig. 3a). In the abandoned farms, Fowler's toads had the most intensive calls in the reservoirs (0.76 ± 0.41). Although their mean calling intensity in the ditches was not statistically lower than the reservoirs (mean=0.43), the large variance of the ditch habitat ($SE = \pm 0.43$) indicated that their activities varied greatly among different locations and they did not show intensive usage in the ditches of abandoned farms.

Compared to the above two species, carpenter frog's abundance in the three habitats exhibited similar patterns in the active and abandoned farms (Fig. 4). However, in the

abandoned farms, they were present in all three habitats; while in the active farms, carpenter frogs avoided the bog habitat as indicated by Figure 4b that they were statistically absent in 100% of the surveyed bogs. In addition, the calling intensity of carpenter frogs in the reservoir habitat was higher in the abandoned farms (1.29 ± 0.09) than the active farms (0.79 ± 0.08).

Lastly, although southern leopard frogs were observed in all habitats of both active and abandoned farms, the large variance of the mean calling intensity indicated that their density varied tremendously among different survey locations (Fig.5a). Statistically they were absent in all three habitats of the active farms (Fig. 5b). Their mean calling intensity was only statistically different from 0 in the reservoir habitat of the abandoned farms (Fig. 5a).

As stated in *Methods*, I examined the chronology of all four species in order to depict their specific peak calling period. One noticeable pattern is the prolonged activities of green frogs in the bog habitat within active farms (Fig.6). They continued to be active until August, while in abandoned bogs their activities diminished in July. This prolonged activity within active farms corresponded with the more persistent water level in the active farms. As shown in Fig.7, the water level within all three habitats of abandoned farms exhibited a steady decrease during a period without precipitation; while in active farms, the water level remained constant. As stated in *Methods*, the water level in the bog habitat was measured indirectly by measuring the water depth of the irrigation side-ditches surrounding the bogs (Fig.7). Therefore, although the mean water level in these side-ditches did not differ significantly between active and abandoned farms ($p=0.163$), the continuous water withdrawal featured in abandoned farms could indicate a

steady decrease of soil water content and a gradually reduced saturation level in the bogs; while the stable water level in the active farms suggested consistent soil water saturation in the bogs. Saturated soil can then provide standing surface water, which is critical for the persistent activities of green frogs in this habitat.

DISCUSSION

This study demonstrated the habitat value of active wetland farms to the anuran communities in the Pinelands of New Jersey. Particularly, this study has shown the importance of the diverse habitats within farms that were utilized by various anuran species with different biological requirements. In addition, compared to the same habitats in abandoned farms, the active cultivation of cranberries was shown to create varied effects to the survival of anurans. Growers' management of the water level in the active farms might have differed anuran's habitat preference and changed their phenology. One species, *Rana clamitans* exhibited higher density associated with longer breeding activities within the active cranberry cultivation bogs compared to the same habitat in abandoned farms. Although a large body of literature has documented the negative relationship between agriculture and anurans' survival on a landscape scale (Bonin *et al.* 1997; Piha *et al.* 2007), my study suggested that on a farmland scale, proper farmland design and management can benefit the conservation of anuran species.

The most intriguing finding of this study was the high density and occurrence of Fowler's toad *Bufo woodhoussi fowleri* and green frog *R. clamitans* in the bog and ditch habitats of active cranberry farms (Figs. 3 & 4). It is widely believed that many agricultural chemicals are harmful to amphibian larvae and adults (Boone & Semlitsch

2002; Griffis-Kyle & Ritchie 2007), which made it a surprising observation that these two species thrived within or adjacent to cultivation beds. One possible explanation is the limited chemical input of cranberry cultivation. The productivity and health of cranberry plants largely relies on the quality of water and soils within the farmland; many common chemicals in farmlands such as nitrogen and phosphorus will cause algal bloom in the water, or undesirable vegetative overgrowth of cranberry plants (Eck 1990; Roper et al. 2004; Sandler & DeMoranville 2008). Therefore, only limited amounts of nitrogen and phosphorus fertilizers are applied annually, while the usage of pesticide is targeted to specific areas with weed or pest outbreaks (Oudemans et al. 2002; Sandler & DeMoranville 2008).

Another factor that might have contributed to the abundance of these two species in active farms is the lower predator pressure. In 2006 during the preliminary study, I conducted a minnow trap survey of the aquatic fauna (large invertebrates and small vertebrates) in two active farms (ACT 1 & 2) and one abandoned farm (ABD 1). I found that the aquatic fauna was dominated by omnivorous mud-minnows *Umbra pygmaea*, and carnivorous species such as sunfish *Enneacanthus spp.*, the giant water bug *Lethocerus americanus* and the water scorpion *Ranatra spp.* On average, there were 2.8/trap of possible predators in the abandoned farm, and 1.3/trap in the active farms. The lower density of predators in the latter suggested that the anuran species might be facing less predator pressures in the active farms compared to the abandoned ones, although the trapping survey did not have enough farm replicates to conduct statistically rigid comparison. This can have contributed to the higher survivorship of Fowler's toad and green frog's tadpoles and consequently caused the higher number of both species in the

active farms.

As shown in *Results*, green frogs exhibited persistent calling activities in the active bogs during late July and early August (Figs 4a & 6). Their activities in the ditch and reservoir habitats did not exhibit different chronologies between the active and abandoned farms (data not shown). The green frog is believed to be a habitat generalist, which can breed in both permanent and temporary water (Werner & McPeck 1994; Campella & Bunnell 2000). This species is relatively more tolerant to agricultural chemicals (Smith *et al.* 2006). In a similar peat bog system, Mazerolle and Cormier (2003) showed that green frogs had the highest density within moderately disturbed bogs that were subjected to mining. They suggested that the constructed ditches within these bogs have provided additional breeding habitats for green frogs. Similarly, my study demonstrated that agricultural activities in cranberry farms have extended the conditions necessary for green frog breeding by providing more stable hydrological conditions. In my study system, green frog had the latest breeding season that coincided with high evaporation in July and August (Table2). Without precipitation, the fast evaporation can quickly reduce soil water content in the abandoned farms (Fig.7). On the other hand, the water level within active bogs was manipulated by irrigation, which ensured a saturated bog surface with patches of standing water. The standing surface water can then function as refugee to attract high densities of green frogs from the surrounding natural habitats drying from fast evaporation.

Different from the above two species, carpenter frogs *R. virgatipes*, and southern leopard frogs *R. sphenoccephala*, exhibited higher activities in the abandoned farms than the active farms (Fig.4 & 5). My results showed that in both active and abandoned farms,

carpenter frogs had a higher calling intensity in reservoirs (Fig.4), which are open water-bodies with ambient floating vegetation. This finding concurred with previous studies that documented the carpenter frog's preference for large permanent waters (Gosner & Black 1957; Zampella & Bunnell 2000). Because of carpenter frog's preference for the reservoir habitat, the water level change in the active reservoirs during the fall might have caused their lower density within the active farms. The large tadpoles of carpenter frogs (max=110mm, Altig et al. 1998) require a very long over-winter developmental period. Thus, when farmers withdraw water from the reservoirs in October to flood the bogs for cranberry harvesting, the fluctuation of water coincides with the period when carpenter frog tadpoles are about to enter their winter torpor. Several weeks later, water will again be withdrawn from the reservoirs to provide frost-protection in bogs during the winter months. Thus, these hydrological disturbances in active reservoirs can negatively affect the tadpoles' survival in the fall and winter.

Similarly, southern leopard frog's poor performance in active farms can also be related to their phenology. This species exhibited very low mean calling intensities and very large variance in the active farms (Fig.5a). Statistically, southern leopard frog was absent in all three habitats in the active farms as well as the bog and ditch habitats in the active farms (Fig. 5b). Being a habitat generalist that occurs in various freshwater habitats, this species' tadpoles were shown to tolerate fish predation (Gregoire & Gunzburger 2008); this species was also shown to be relatively chemical resistant (Boone & Semlitsch 2002). Therefore, this species' poor performance is probably due to their early breeding season, which coincide with the intensive cultivation activities in the farms. In my study system, southern leopard frogs had the earliest breeding behavior, that

their calls were detected as early as March and began to peak in April. This peak breeding period coincides with the time when growers terminate the winter flooding and drain the standing water from the cultivation bogs. April and May is also the period when growers have the most intensive cultivation. Therefore, these cultivation activities might have interfered with the breeding of the leopard frog, resulting in their low occurrence in the active farms.

In conclusion, in this study I used field observation to demonstrate that the mosaic habitats within wetland farms can be selectively used by four anuran species. Farming activities can largely modify the farmland habitat factors, which was shown in this study as the altered hydrology and the differed predator density. These habitat modifications can be beneficial or detrimental to species with varied biological needs. My study suggested that cranberry farming can provide amiable habitats for anuran species during adverse natural conditions; however it is also critical for farmers and conservation practitioners to create less-disturbed waterbodies as refuges for breeding or metamorphosis during intensive cultivation. In this paper, I intended to relate the observed anuran species' dynamics to the biological traits of these species, but our knowledge of these species is still too limited to fully decipher the mechanisms behind the observation. The interactions among habitat factors can further hinder of abilities to interpret the effect of human activities on each species (Werner & McPeck 1994; Smith et al. 2006). Thus, such in-situ studies in the farmland are necessary for us to directly observed anuran species' response to different human cultivation activities. Farmers and conservationists can then enact proper management strategies in order to maximize the farmland's wildlife habitat function and minimize the negative effects from farming

practices.

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Table 1. Study sites' name and the number of surveyed locations of each habitat type.

Sites	bog	ditch	reservoir
Act1	13	9	4
Act2	8	4	5
Act3	14	13	7
Abd1	15	4	6
Abd2	18	3	4
Abd3	11	5	2

Table 2. Each species' peak calling intensity period based on the three-year survey results.

	Carpenter frog	Southern Leopard frog	Green frog	Fowler's toad
Peak months	May—July	April—1 st week of July	June-August	May-July

Table 3. Summary of top models for each species. $\Delta AIC > 2$ is used as selection criteria for the top models. Colum “Top model” shows the combination of the latent probability distributions in the top model. “Detectability parameters” indicate the restrains of the detectability parameters (e.g. 1,2,2,1,1,1 means $p_2=p_3$, $\beta_{21}=\beta_{31}=\beta_{32}$). “ ΔAIC ” is the AIC difference between the top model and the model with the next lowest AIC.

	Top model	Detectability parameters ($p_1, p_2, p_3, \beta_{21}, \beta_{31}, \beta_{32}$)	ΔAIC
Carpenter frog	farm+habitat+interaction	1,2,3,1,1,1	6.9
S Leopard frog	farm+habitat+interaction	1,2,2,1,1,1	75.95
Green frog	farm+habitat+interaction	1,2,3,1,1,1	14.2
Fowler’s toad	farm+habitat+interaction	1,2,2,1,1,1	10.0



Figure 1: Aerial-photo of farm Act3. Arrows indicate the three habitats. A: bogs (cultivation beds. The surrounding side ditches for each bog is not visible on this photo). B: ditch (main irrigation ditch). C: reservoir.

Green frogs

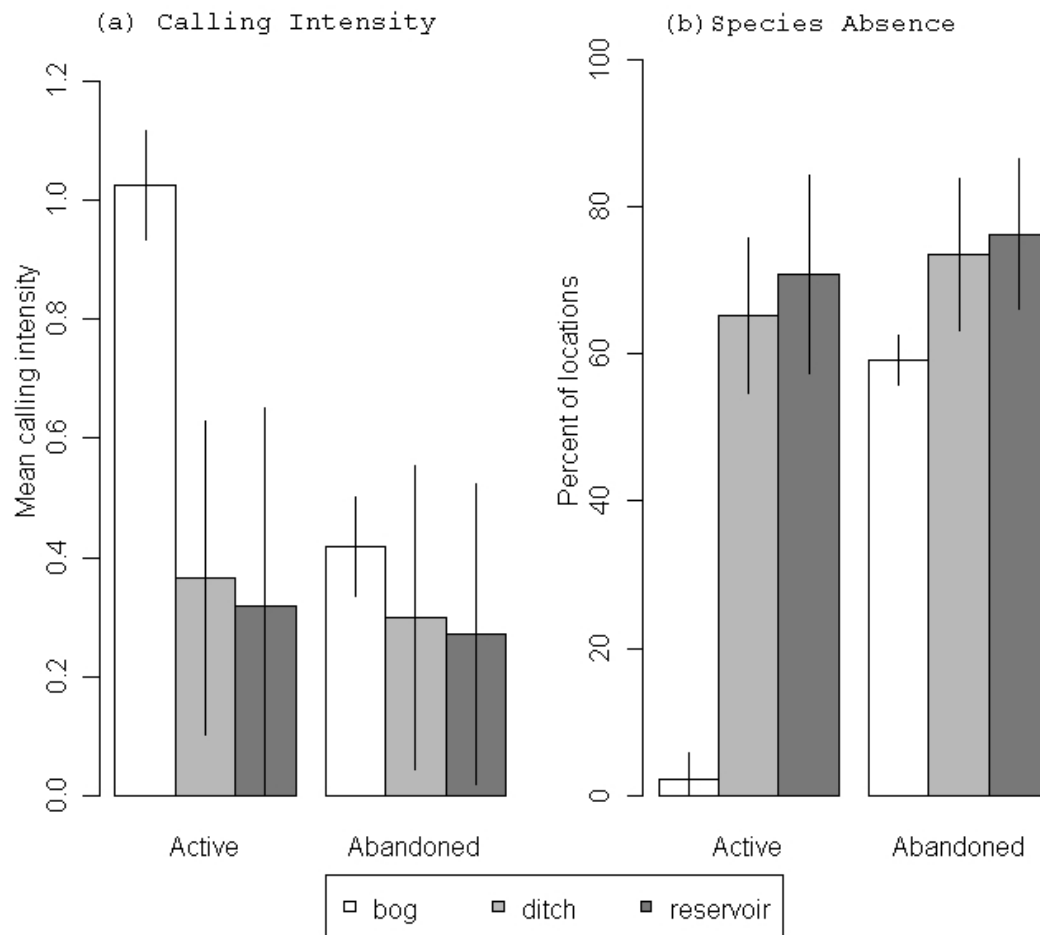


Figure 2. Green frogs (*R. clamitans*). (a) Mean density of green frogs in bogs, ditches and reservoirs within active and abandoned farms. (b) Percent of survey locations where green frogs were absent. Error bars indicate the standard error (\pm SE).

Fowler's toads

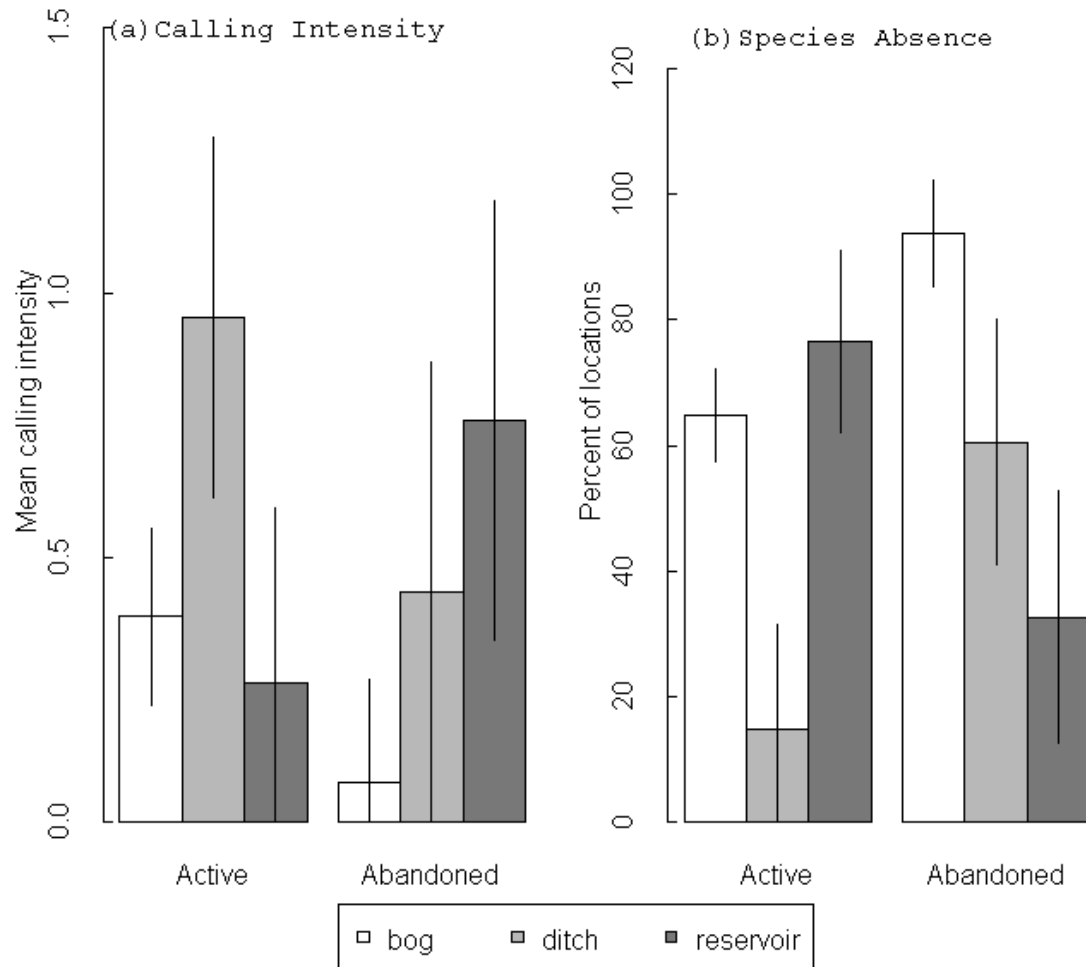


Figure 3. Fowler's toads (*Bufo woodhousii fowleri*). (a) Mean calling intensity of Fowler's toads in bogs, ditches and reservoirs within active and abandoned farms. (b) Percentage of survey locations where Fowler's toads were absent. Error bars indicate the standard error (\pm SE).

Carpenter frogs

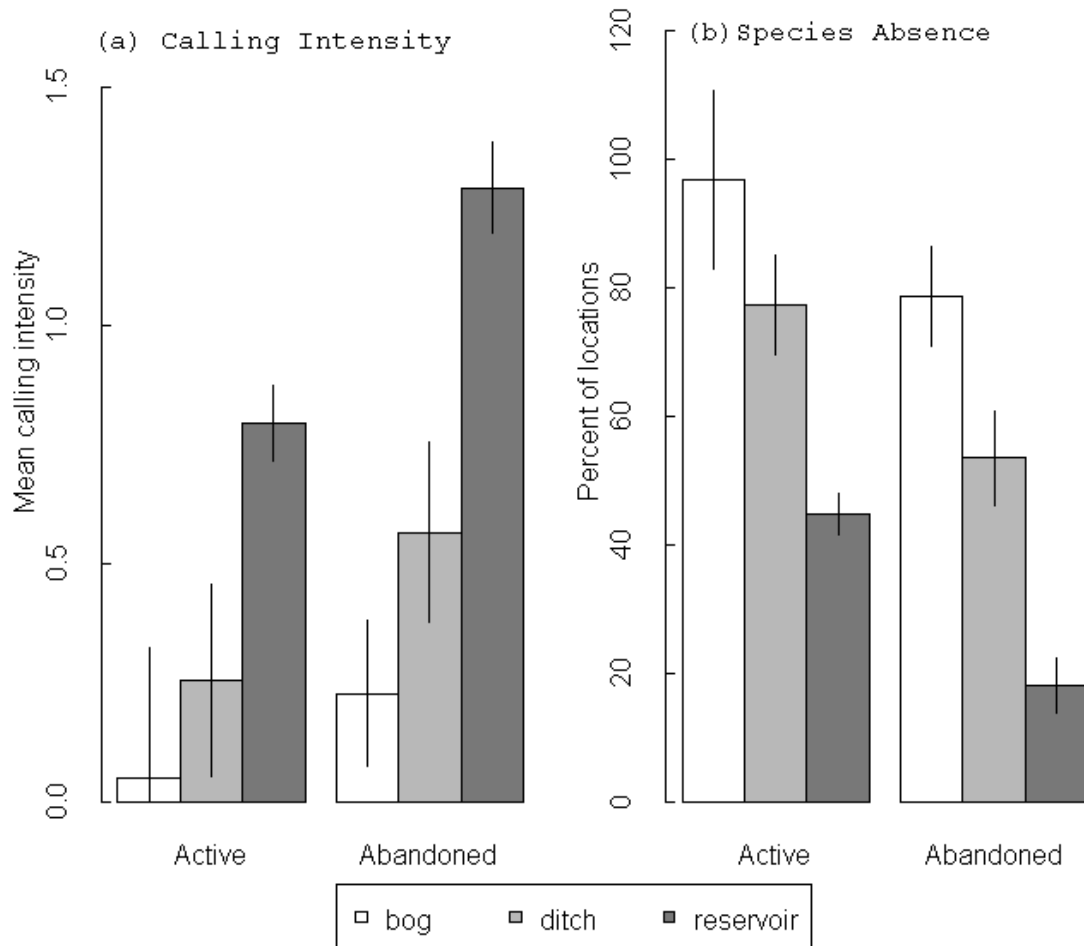


Figure 4. Carpenter frogs (*Rana virgatipes*). (a) Mean density of carpenter frogs in bogs, ditches and reservoirs within active and abandoned farms. (b) Percentage of survey locations where carpenter frogs were absent (i.e. probability of $N=0, \psi^0$). Error bars indicate the standard error (\pm SE).

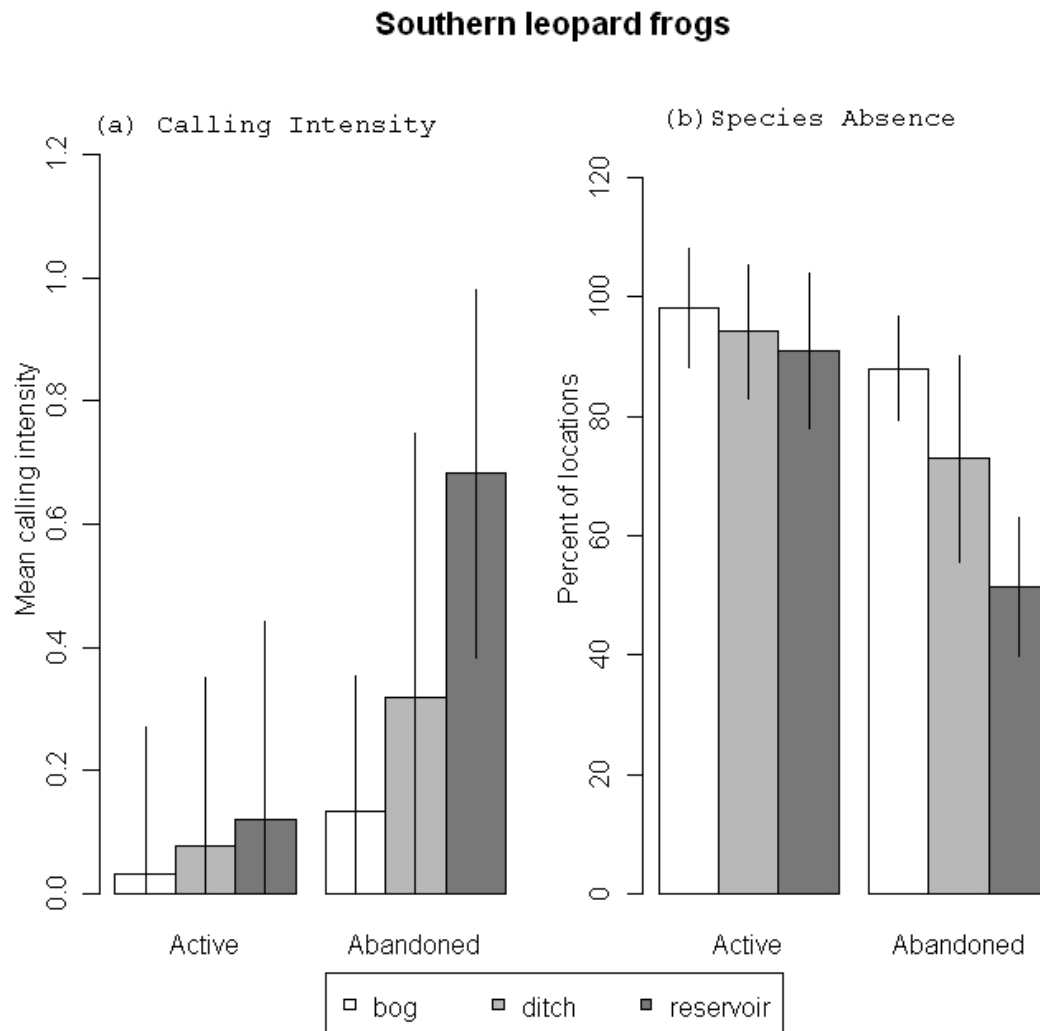


Figure 5. Southern leopard frogs (*R. sphenoccephala*). (a) Mean calling intensity of southern leopard frogs in bogs, ditches and reservoirs within active and abandoned farms. (b) Percentage of survey locations where southern leopard frogs were absent. Error bars indicate the standard error (\pm SE).

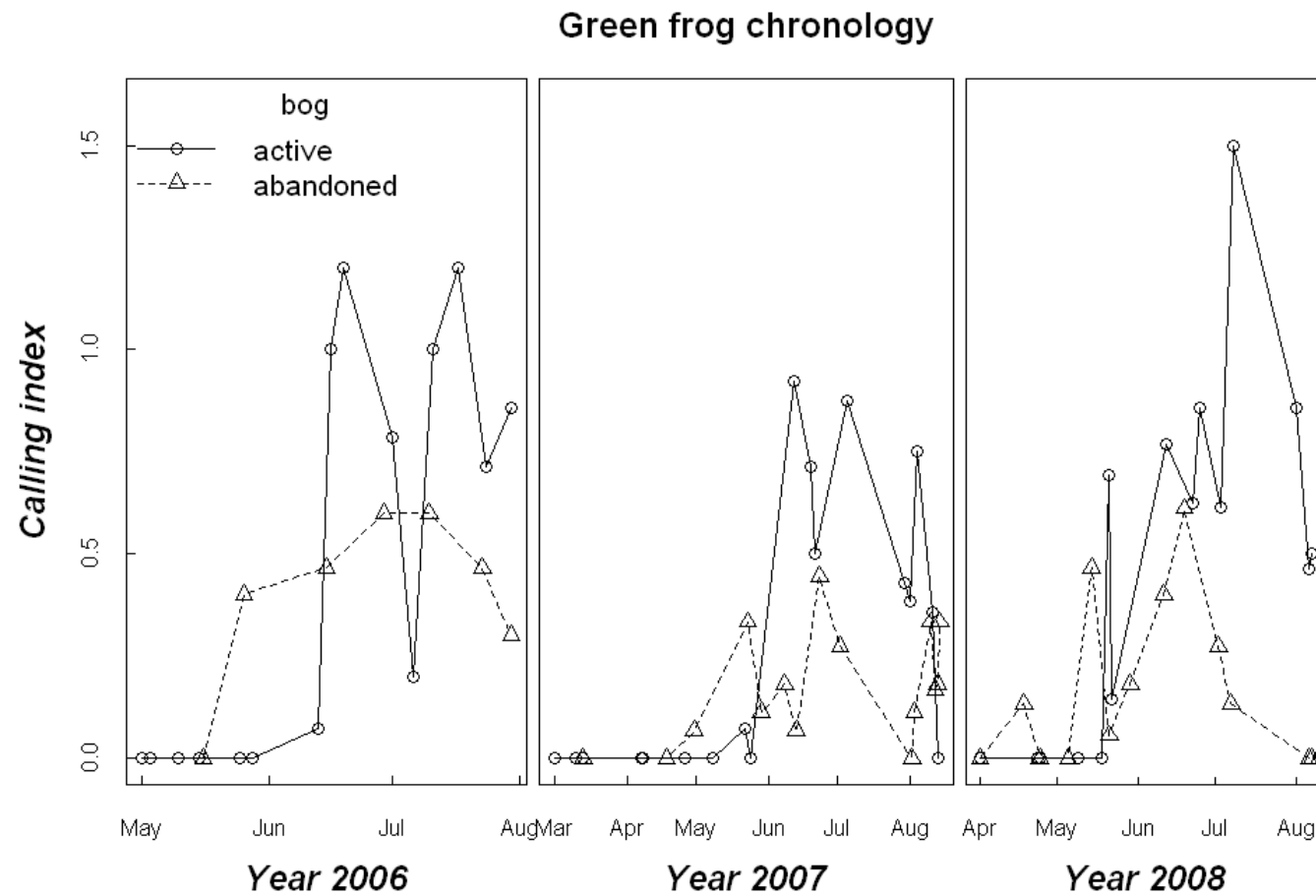


Figure 6. Calling intensity of green frog (*Rana clamitans*) from May 2006 to August 2008. The calling index is the averaged calling intensity for all surveyed locations.

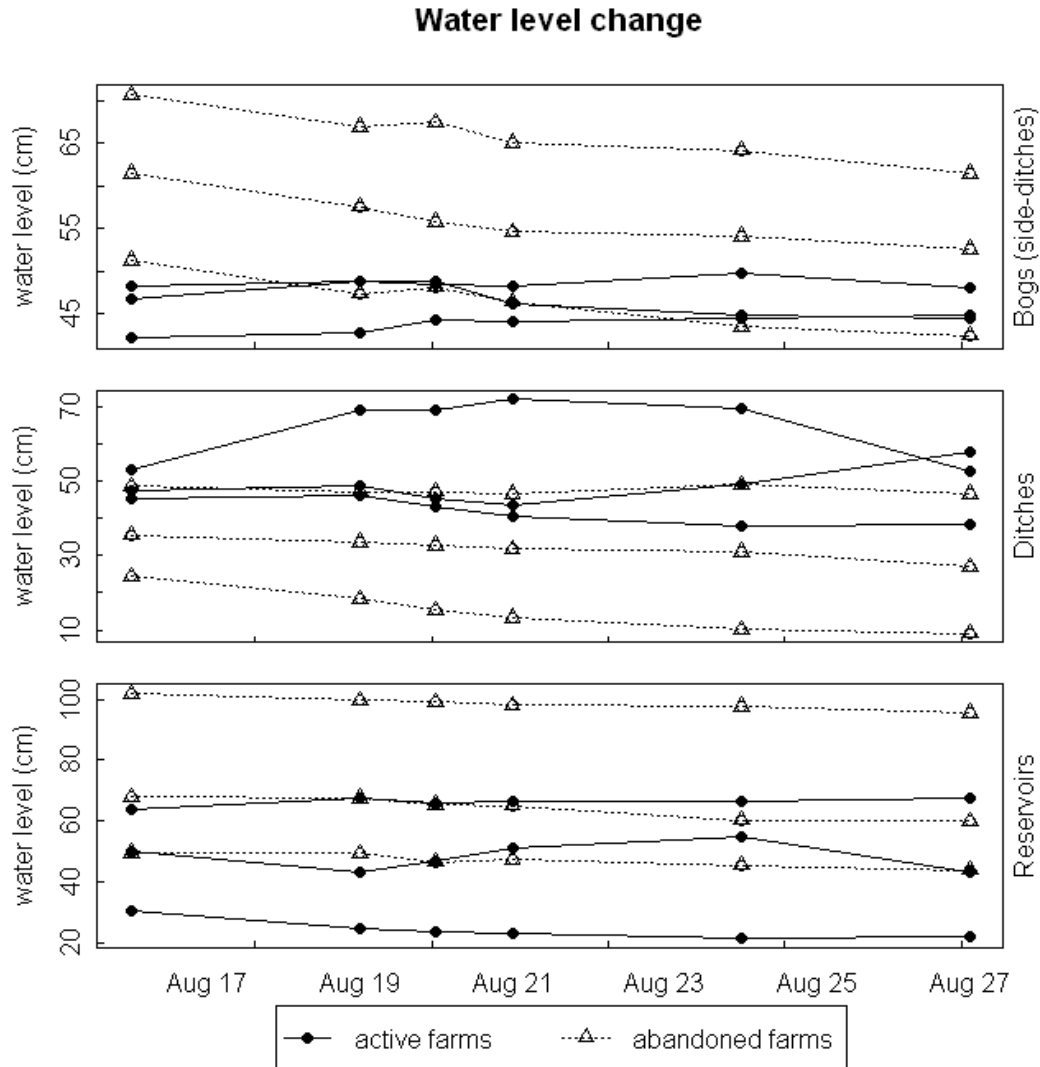


Figure 7. The fluctuation of water level in active and abandoned farms. Each line represents a farm (active or abandoned), and each data point shows the mean water level from three independent measuring points. The repeated measurement analysis showed that the time effect for all three habitats in active farms was not significant (p -value = 0.83, 0.93, and 0.49 for the bog, habitat and reservoir, respectively). On the contrary, the time effect for all three habitats in abandoned farms was significant; the p -values of the bog, ditch and reservoir habitat is $7.368\text{e-}09$, $5.407\text{e-}04$, and $2.255\text{e-}07$, respectively. There was no significant difference between the water levels of the active or abandoned farms for all three habitats (the p values were 0.163, 0.156, and 0.289, respectively).

APPENDIX

1. Detectability parameters (adopted from Royle and Link 2005):

	$f(y=0 N)$	$f(y=1 N)$	$f(y=2 N)$	$f(y=3 N)$
$N=0$	1	0	0	0
$N=1$	β_{10}	p_1	0	0
$N=2$	$(1-\beta_{21})*(1-p_2)$	$\beta_{21}*(1-p_2)$	p_2	0
$N=3$	$(1-\beta_{31})*(1-\beta_{32})*(1-p_3)$	$\beta_{31}*(1-\beta_{32})*(1-p_3)$	$\beta_{32}*(1-p_3)$	p_3

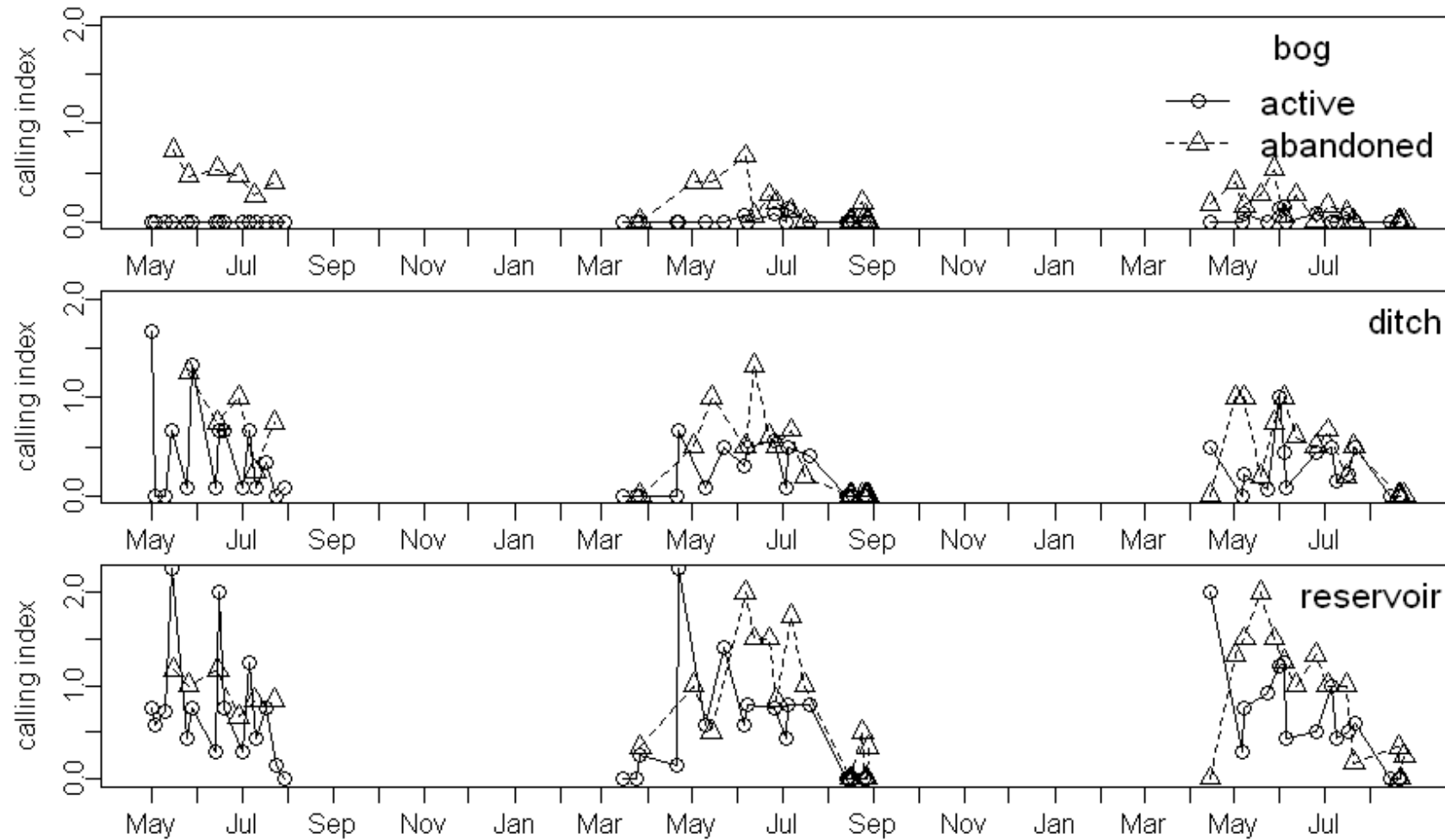
In the table, parameters p_1 , p_2 and p_3 are the correct classification probabilities. β_{jk} are the conditional misclassification probabilities: the probability that observing a calling intensity “k” given that the true intensity is j and $y \leq k$.

2. Candidate models for each species’ latent abundance classes.

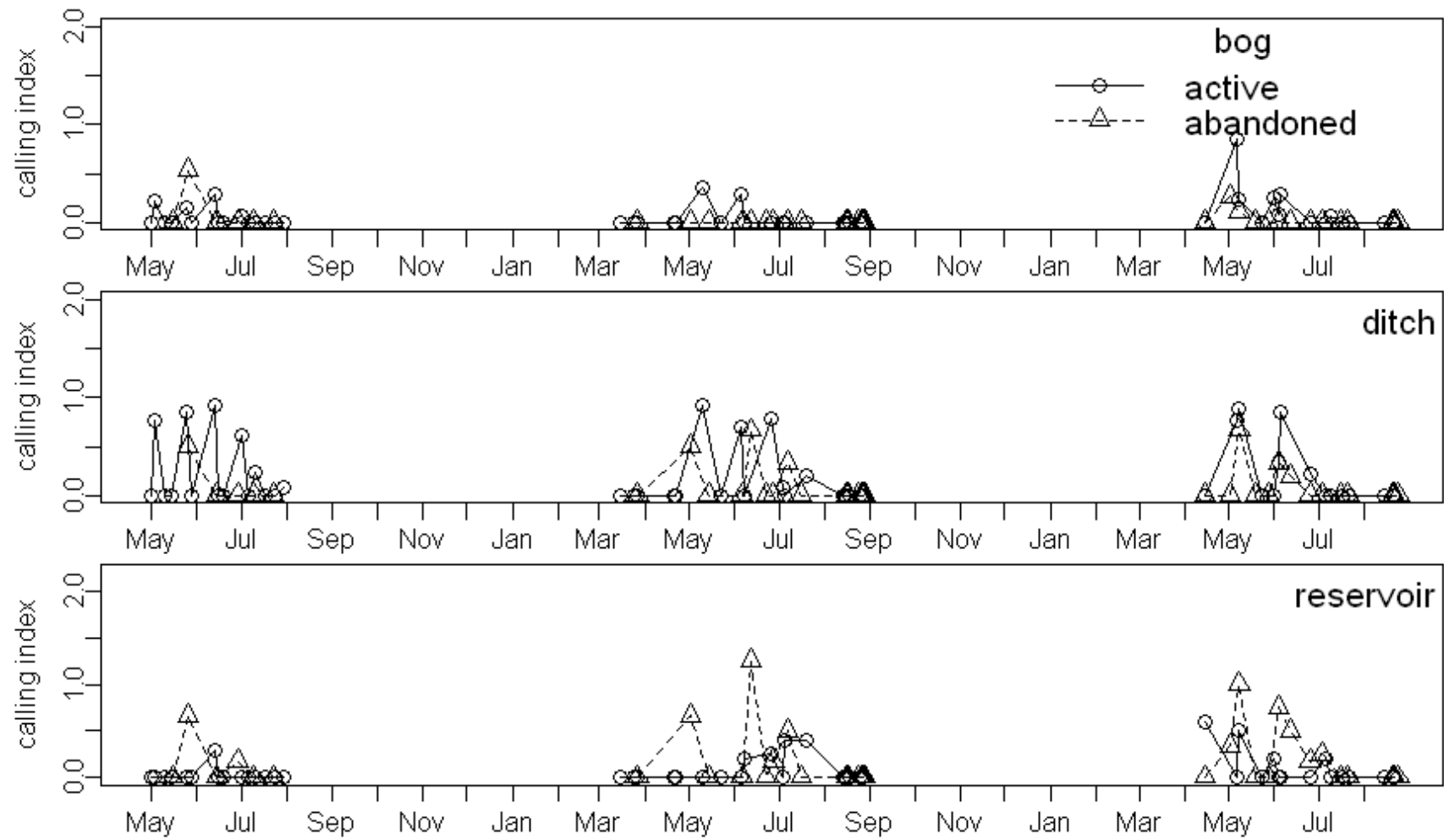
- 1) $\text{logit}(\psi_l^{k=0,1,2,3})$ $l = 1$ or 2 for active or abandoned farms. The abundance distribution is determined by farm status.
- 2) $\text{logit}(\psi_m^{k=0,1,2,3})$ $m = 1, 2$, or 3 for bog, ditch and reservoir. The abundance distribution is determined by habitat types.
- 3) $\text{logit}(\psi_l^{k=0,1,2,3} + \psi_m^{k=0,1,2,3})$ The abundance distribution is determined by both farm status and habitat types.
- 4) $\text{logit}(\psi_l^{k=0,1,2,3} + \psi_m^{k=0,1,2,3} + \psi_{l,m}^{k=0,1,2,3})$ The abundance distribution is determined by both farm and habitat types, as well as an interaction term between them.
- 5) $\text{logit}(\psi^{k=0,1,2,3})$ There is only one abundance distribution for all the habitats and farms. Neither farm nor habitat has an effect on the anuran’s abundance.

3. Chronology of all four species in year 2006, 2007, 2008.

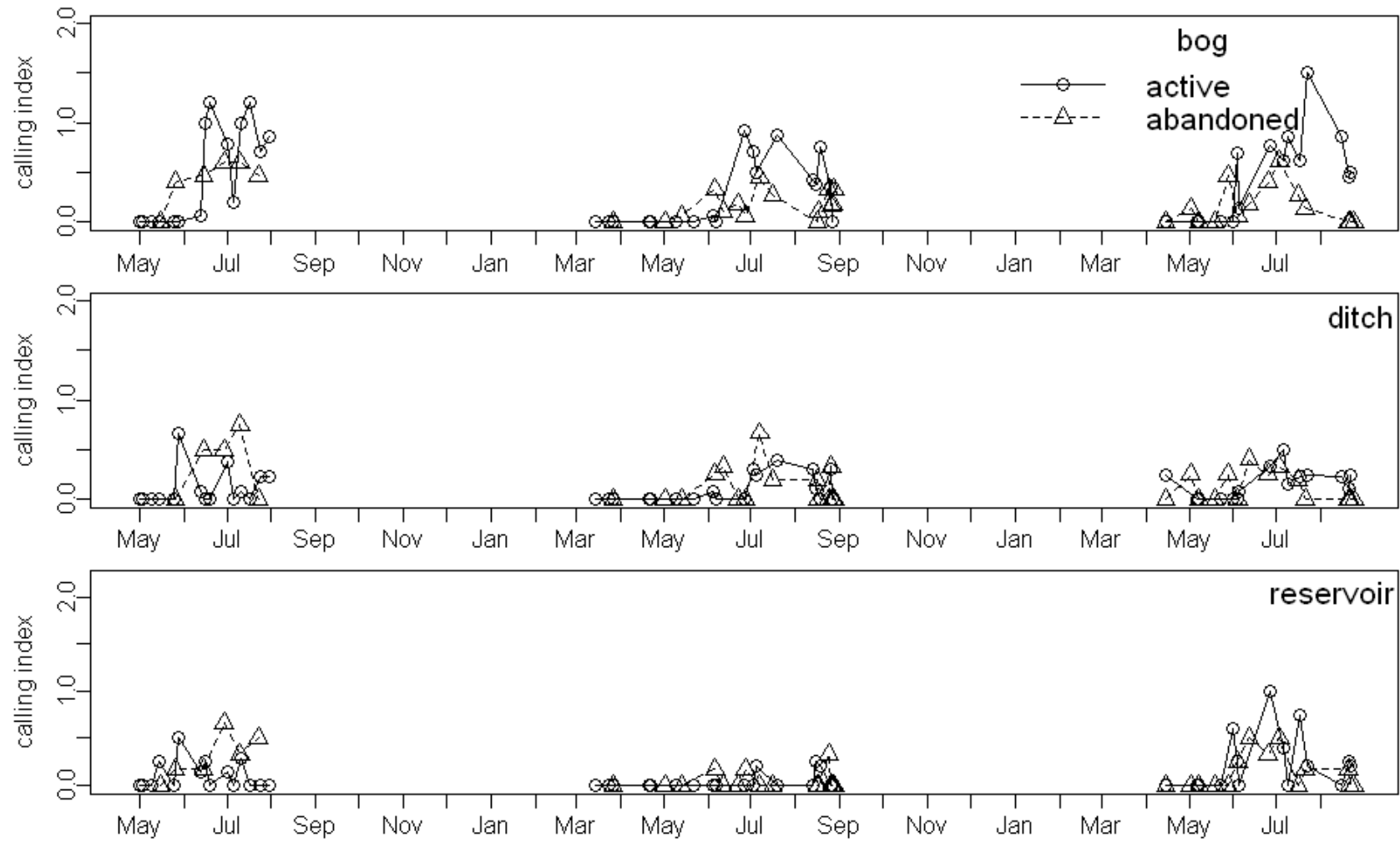
Carpenter Frog



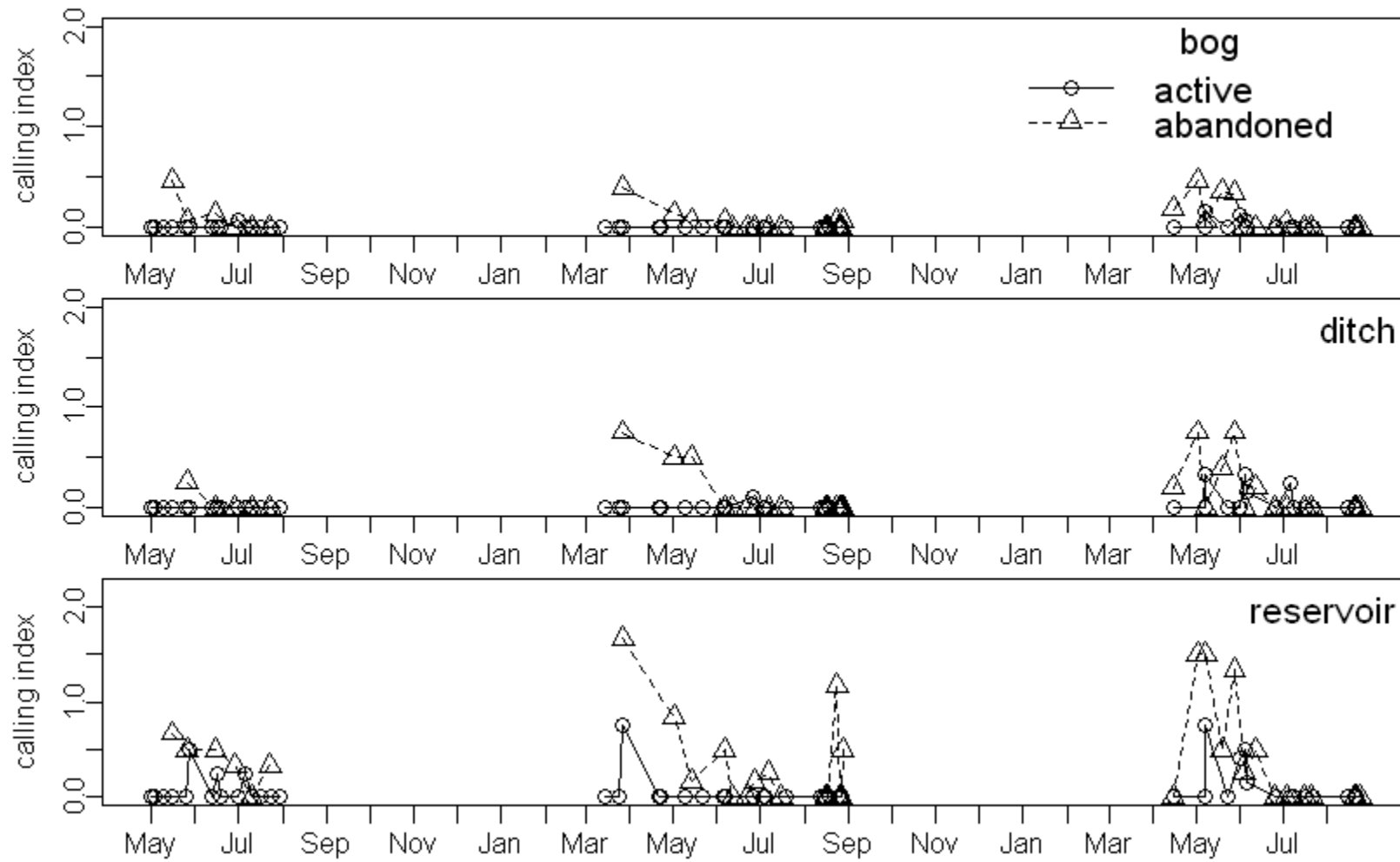
Fowler's toad



Green Frog



Southern Leopard Frog



CHAPTER 2

Seed bank heterogeneity in a post-agricultural wetland system: implication for restoration

ABSTRACT

Restoration of natural communities in wetlands previously used for cranberry agriculture poses problems not present when restoring upland agricultural areas, because of the need to manage wetland hydrology and persistent agricultural woody tissue. I conducted two factorial experiments to determine how post-agricultural abiotic and biotic legacies affect the ability of the seed bank in abandoned cranberry bogs to produce diverse native communities. To determine how hydrology influences seed bank germination, I selectively flooded soil acquired at different depths in cranberry beds with different ground water table heights. In order to determine the role of ground cover in seed bank germination, I also compared germination under two common weed colonies and remnant cranberry tissues and tested the effect of ground cover removal. Results of the experiments demonstrated that the post-agricultural edaphic conditions, including soil hydrology and soil depth, are the major factors determining the seed bank viability, species composition and germination density. Flooding treatments increased the germination density but did not significantly change seed bank's germination probability or the species composition. On the other hand, ground cover removal was an effective method to reduce the interference from weed colonies and cranberry remnant tissues. Removal increased germination density, regardless of the type of existing ground cover. I conclude that to restore post-agricultural wetland habitat, it is necessary to enact flexible restoration strategies corresponding to heterogeneous post-abandonment conditions.

KEY WORDS

Wetland agriculture; Seed bank; Succession; Flooding; Soil depth; Ground cover removal

1. INTRODUCTION

Farmland abandonment is increasing globally as a result of intensified agricultural practices, increased soil degradation due to chemical abuse, and various social or economic crises (Cramer and Hobbs 2007). Increased awareness of plant communities' environmental functions has accelerated the study of succession and restoration in abandoned farmland (Myster and Pickett 1994; Knops and Tilman 2000; Harmer *et al.* 2001; Foster *et al.* 2004). It is believed that restoration and secondary succession essentially share the same ecological foundation (van der Valk 1998; Walker *et al.* 2007). Therefore, people have used natural succession with human assistance, such as flooding and ground cover removal, as a low-cost and effective way to conduct restoration (a.k.a. passive restoration. Pywell *et al.* 1995; Verhagen *et al.* 2001). However, most studies on post-agricultural succession have been conducted in abandoned upland farms. We have very limited knowledge about the plant community development in post-agricultural wetlands, although globally there are a broad variety of agricultural-disturbed wetlands that are in urgent need of restoration, such as rice paddies in Asia (Yamada *et al.* 2007), fens and bogs in northern Europe and “prairie potholes” in the Great Plains of North America (Wheeler *et al.* 1995).

In this study, I aimed to determine how wetland agricultural history has affected the seed bank composition in abandoned wetland farms; and how agricultural legacy effect modify the seed bank germination. The study was conducted in an abandoned cranberry

(*Vaccinium macrocarpon*) farm which was originally excavated from wetlands in the Pinelands of New Jersey, where cranberry is a native plant. Cranberry farms are composed of multiple cultivation beds (hereafter “cranberry bog”), which are leveled to be lower than the original ground surface. After a bog is excavated, woody cranberry cuttings (hereafter “runners”) are planted on a layer of sand that is overlaid on the organic horizon of the initial wetland soil. A new layer of sand is added every three years to bury the runners, stimulating crop production (Eck 1990). As a result, the soil profiles of abandoned bogs are composed of alternating strata of sand and decomposed organic material, and the soil accumulated during cultivation can be clearly separated from the original wetland organic soil.

I first examined the seed bank viability and composition at different soil depths. The seed bank can potentially be used as propagule sources during restoration (Hausman *et al.* 2007). However, after years of cranberry cultivation, it is unknown what proportion of seed bank within the disturbed soil layers is upland species or agricultural weed (Leck and Leck 1998; Cramer and Hobbs 2007). It is also intriguing to test the viability of the original seed bank in the soil layers beyond the depth of accumulated soil, to examine whether the seeds can be germinated under many years of submerging and being exposed to agricultural chemicals.

Secondly, I investigated the seed bank composition under different hydrological conditions in the landscape. Within the farm, cranberry bogs are located across the landscape at different distances from the water source. Hence, before the bogs were constructed, the original wetland vegetation and seed bank exhibited spatial variation as a result of different saturation and flooding frequencies, water depth and soil moisture

(Zampella *et al.* 1992; Hupp and Osterkamp 1996). During cranberry cultivation, the water table is actively managed to achieve homogeneous and synchronous flooding (Eck 1990) through the creation of water control structures from the reservoir to supply surface water to the bog complex. After abandonment, the bogs' hydrology is not actively managed. As a result, different bogs in the farm can again resume different hydrologic regimes (mean water table depths, frequencies and depths of flooding) as a result of the varied distances from the water source. It is not known whether the manipulation of hydrology during cultivation has modified the seed bank composition or if cranberry bogs still possess different seed sources that existed before the farm construction at different distances from the water source.

Thirdly, in order to seek proper restoration strategies, I selectively applied flooding on the soil samples. The frequency and depth of flooding is often believed as the primary determinant of plant survival (Cronk and Fennessy 2001; Fraser and Karnezis 2005) and community composition in wetlands (Casanova and Brock 2000). My experiment aimed to compare whether flooding changed the germination rate, density or the species composition in post-agriculture wetlands.

In addition to the abiotic agricultural legacy effects, in abandoned agricultural habitat, the interference of remnant crop tissues (Ferguson *et al.* 2003) and the competition from remaining agricultural weed species (Rejmanek and Leps 1996) can slow the pace of the consequent succession. Both forms of interference can be observed in abandoned cranberry farms. Following abandonment, woody cranberry runners persist as a thick layer. The areas that are covered by less dense runners are usually occupied by scattered but dense clones of common cranberry weeds, including sedges (*Carex spp.*) and

Carolina redroot (*Lachnanthes caroliana*) (Beckwith and Fiske 1925). I hypothesized that the remnant cranberry runners and the vegetative propagation of the weed species interfere with other species' germination from the seed bank, leading to competitive exclusion. I tested the hypothesis using a ground cover removal experiment.

In summary, this study used two experiments to investigate the abiotic and biotic factors that potentially affect the early stage of secondary succession in abandoned wetland farms. The study will provide an informative guide to establish healthy local plant communities in abandoned wetland farms.

2. METHODS

2.1 Study sites:

The experiment was conducted at the Franklin Parker Preserve (39.80479N, -74.54841W), a 3,798 ha area in the heart of the Pinelands National Reserve. The preserve includes 450 ha of abandoned cranberry farm, the former DeMarco Farm. This farm was mainly constructed in 1940s, and cultivation was terminated in the late 1990s. The cranberry farm was developed on hydric mineral soils (Atsion and Berryland series—sandy, siliceous, mesic Aeric Alaquods) which have a thick organic horizon overlying an organic-rich sandy A horizon.

2.2 Field sampling and greenhouse germination:

2.2.1 Experiment 1: effects of the bog hydrology and soil depth on seed bank germination:

In June 2007, soil cores (diameter and length = 15cm) were taken from 8 abandoned cranberry bogs. In order to avoid germination from the seed bank preceding the sampling, soil cores were taken in areas where the ground was covered by cranberry runners while

had no existing plants. Previous water table measurements from May to July 2006 showed four bogs (hereafter as “wet bogs”), which are closer to the reservoir, had relatively high water tables (average depth= $-13.8 \pm 5.4\text{cm}$), compared to the other four bogs’ water tables (hereafter as “dry bogs”), which are closer to the upland (average = $-60.7 \pm 12.0\text{cm}$). In each bog, 4 soil cores were taken near the center of the bog (except in one wet bog, 6 soil cores were taken). In the greenhouse, each soil core was divided into three layers: the bottom layer included the pre-agricultural wetland soil, the middle layer included the agricultural strata, and the top soil included the most recent cultivation medium that has been exposed after bog abandonment. Subsamples of equal amounts (thickness) were taken from each layer in order to compare the germination from equal quantities of soil. Each subsample was evenly spread onto a 25cm x 25cm greenhouse germination tray over 1cm sterile potting soil, which was underlain by 1cm of sand. The trays were placed on a mist bench with a 6-minute misting interval. Soils from half of the samples from each bog were flooded every other week by filling up the tray with 2cm water for a week (flooding treatment), while the other half of the soils were never flooded (non-flooding treatment). In order to maintain the water level in the flooded trays, both flooding and non-flooding treated trays were kept under the mist-bench, and the water level was examined periodically during the week to ensure the merging of the soil surface. There were a total of 102 trays (34 cores * 3 layers). The germinated seedlings were harvested and identified throughout the growing season until the end of October, 2007.

Because many trays had no germination, I applied a Bayesian Zero-inflated Poisson model (ZIP model, section 2.3.2) to analyze the effect of bog hydrology, soil layer and flooding treatment on germination. ZIP model is able to separately model the possibility

of seed presence and the density of germination where seeds are present. The community composition of germinants was analyzed using Non-metric Multidimensional Scaling (NMDS, section 2.3.1). The relationship between species composition (i.e. the NMDS output) and the experiment factors (i.e. hydrology, soil layer and flooding) was assessed using a Bayesian normal linear model (section 2.3.2).

2.2.2 Experiment2: effects of ground cover removal on seed bank germination:

In June 2008, soil blocks (25cm X 25cm X 4cm) were excavated from abandoned cranberry farms with three types of ground covers: Runner, *Carex* and *Lachnanthes*. “Runner” areas had no living vegetation, but were covered with dense woody cranberry runners. “*Carex*” areas were covered with dense *Carex striata* and sparse cranberry runners, while *Lachnanthes* areas were covered with dense *Lachnanthes caroliana* and sparse cranberry runners. Four replicate sites were used for each ground cover type. Within each site, 3 (Runner) or 5 (*Carex* and *Lachnanthes*) soil blocks were taken, on which different removal treatments were applied in the greenhouse (see Table1). Except the last treatment, the removal of runners and plants was done by clipping the above ground tissue without disturbing the soil. Table 1 summarizes the treatment codes used in the analyses below.

Soil blocks were kept in the greenhouse from June to October, 2008, and the plants germinated in each block were identified and counted. The relationship between number of seedlings and treatments was analyzed using Bayesian normal linear model because the number of seedlings from each block exhibited a normal distribution. The full model included the effects of (1) removal treatments; (2) ground cover types; (3) the interaction between treatments and cover types. A stepwise model selection criterion was used to

choose the most parsimonious model (section 2.3.2). As in the first experiment, I then used NMDS ordination and a Bayesian normal linear model to analyze the effects of ground cover types and removal treatments on species composition (section 2.3.1).

2.3 Statistical Analysis:

2.3.1 Non-metric Multidimensional Scaling (NMDS):

In both experiments, Non-metric Multidimensional Scaling (NMDS) was used to construct the ordinations to compare the species compositions. NMDS is a widely accepted method used to study community composition and was especially preferred in this study because of the non-normally distributed germination of each species (McCune and Grace 2002).

The NMDS analysis was conducted using R (Vegan library in R version 2.8.0) based on the Bray-Curtis distance among the observations (Zuur *et al.* 2007). Final stress < 0.20 was used as the rule to determine the optimality of the ordination (McCune and Grace 2002). Because NMDS aims to characterize the community structure, trays that had no germination were excluded from the analysis.

2.3.2 Bayesian Generalized Linear model: Normal Linear model and Zero-inflated Poisson model

Bayesian Generalized Linear Model (GLM) is a strong statistical tool to analyze predictor variables' effects on dependent variables. It is a flexible and accurate tool to analyze data with complex or discrete structures (Congdon 2001). In this study, I applied Bayesian Normal Linear Model and Bayesian Zero-inflated Poisson model based on the nature of the observed data.

The NMDS scores of both experiments and the total germination of experiment 2

were analyzed using a Bayesian Normal Linear model. Specifically, a model with experiment 1's NMDS output as dependent variable was analyzed against the effects of bog hydrology, layer, flooding and their full factorial interactions. Similarly, the total germination and NMDS output of experiment 2 were analyzed as dependant variables, against the effects of ground cover type, removal treatments, and their interactions. These models were implemented in WinBUGS 1.4 (Imperial College & MRC) with a noninformative normal prior for the dependent variable and regression coefficients. To avoid over-parameterizing, stepwise model selection was used to select reduced models (Burnham and Anderson 2002). Each model was ranked using the Deviance Information Criterion (DIC, Bayesian analog of AIC). The top model's 95% credible interval (CI, analog of confidence interval) for each factor was used to determine whether the factor had a significant effect (namely, whether the interval overlapped with 0).

The total germination from the first experiment was analyzed using a Bayesian Zero-Inflated Poisson (ZIP) model because the germination result followed a Poisson distribution with excess zeroes. A ZIP is a model that uses two independent underlying distributions: (1) a binomial distribution to model the probability of the presence of germination (i.e. seedlings); and (2) a Poisson distribution to model the density of germinated plants where viable seeds are present. The binomial probability and the Poisson mean are modeled separately as linear functions of the predictor variables to test these variables' effects on germination occurrence and density, respectively. Non-informative priors were given to these variables and the 95% CI of their posterior distribution was used to determine whether the effect was significant. Because the 102 data points were not enough to include all interactions of the main effects into the ZIP

model, I cannot use the DIC criterion to select the most parsimonious model to avoid over-parameterizing the model. Therefore, only the main effects were included in the ZIP model to examine the effect of soil depth, hydrology and flooding on germination probability and germination density.

3. RESULTS

3.1 Effects of Bog hydrology, soil layer and flooding on seed bank germination

3.1.1 Germination probability and density:

Out of the 102 trays, 69 (67.6%) showed germination, with an average of 11.4 seedlings per tray (ranging from 1 to 86 seedlings/tray). As shown in Figure 1a, the model result showed that the probability of observing seed germination in wet bogs ($81\% \pm 5\%$) was higher than in dry bogs ($57\% \pm 8\%$). However, in trays where viable seeds did exist (i.e. where germination was observed), the plant density was higher in dry bogs (13.1 ± 0.8 seedlings/tray) than in wet bogs (10.8 ± 0.5 seedlings/tray). Similarly, only 43% of trays from the bottom layer exhibited germination, which was significantly lower than the top ($75.9\% \pm 7\%$) and middle layers ($81.9\% \pm 6\%$). However, the germination density of the bottom layer (14.3 ± 1.1 seedlings/tray) was significantly higher than the top (10.9 ± 0.6 seedlings/tray, Figure 1b) and the middle layer (11.2 ± 0.7 seedlings/tray). Lastly, the flooding treatment did not change the probability of germination presence (flooding $70\% \pm 6\%$; non-flooding $68\% \pm 6\%$), but the germination density in flooded trays was 2.9 seedlings/tray higher than the non-flooding treatment.

3.1.2 Species composition:

Twenty-three species were observed in the experiment. Three species were not identifiable until October 2006 when the experiment ended (one monocot and two dicots).

These species were ordinated using four NMDS axes resulting in a stress measurement of 0.15, which is within the range of “fair ordination” (0.10 to 0.20) of typical ecological studies (McCune & Grace, 2002). Overall, 85.2% of the variance was explained by the four axes. NMDS1 itself accounted for 47.5% of the variance, while NMDS4 only explained 9.9% of the total variance.

As shown in Figure 2, bog hydrology and soil layers exhibited strong effects on species composition. Along NMDS1 the germination from wet bogs (filled symbols) and dry bogs (open symbols) are clearly separated (the mean difference between wet and dry bogs is $\Delta \text{NMDS1} = 0.61 \pm 0.07$). The three layers' species composition is separated along NMDS2 (top-middle $= 0.29 \pm 0.08$; top-bottom $= 0.61 \pm 0.13$; middle-bottom $= 0.31 \pm 0.13$).

The ordination plot of the species scores revealed clusters corresponding to the trays from the bottom layer of the wet bogs (Figure 2 (a) and (b)). This cluster is composed of *Cyperus retrorsus*, *Drosera rotundifolia*, *Lachnanthes caroliana*, *Eleocharis flavescens*, one *Juncus sp.* and one *Hypericum sp.* (St. John's Wort). The four identifiable species are listed as “obligate wetland” or “facultative” wetland species (U.S Fish & Wildlife Service, 1996). The species composition of flooded and non-flooded trays had no significant difference along NMDS1 or NMDS2. Their difference along NMDS3 was significant ($\Delta \text{NMDS3} = 0.19 \pm 0.07$), but since NMDS3 only accounted for 11.6% of the variance, this result suggested that flooding treatment did not have a strong effect on the species composition compared to the bog hydrology and soil layers.

3. 2 The effects of cranberry runners and pioneer species on seed bank germination:

3.2.1 Germination density:

There were 283 seedlings that germinated. Table 2 shows the DIC of candidate models that were used to model the density of germination. The top model included the main effects of cover type and removal treatment. However, the Δ DIC of the model that only include removal treatment (model 2) was 1.8. It is believed that models with Δ DIC<2 have an equally good fit as the top model. This suggests that removal is an important parameter to model the germination density. Although adding cover type to the model slightly increased the model's fit, the effect was not very strong. The high Δ DIC of the full model indicated the interaction between ground cover and removal treatment was not important to explain the variation of germination density (Table 2). Therefore in Figure 3b and 4a, the removal of *Carex* and *Lachnanthes* were lumped together to examine the effect of ground cover removal.

The top model's posterior distribution was used to investigate the effects of ground cover and removal treatment (Figure 3). Compared to soil blocks covered with runners, *Lachnanthes* cover significantly reduced the germination density, and *Carex* cover had an intermediate but non-significant effect. In addition, figure 3b showed that all removal treatments increased the total number of germinated seedlings compared to the control blocks. However, there was no significant difference among these four removal treatments.

3.2.2 Species composition:

Fifteen species were observed in the experiment. Three NMDS axes were used to attain a final stress=0.164. The three NMDS axes explained 56.6%, 17.8%, and 14.1% of the variance. The Bayesian Normal Linear model showed axis 1 was strongly related to the different removal treatments and axis2 was related to the ground cover types (Figure

4 (a) and (b), respectively). The runner removal treatment (P+R-) significantly changed the species composition along axis 1 compared to the control ($\Delta \text{NMDS1}=0.34 \pm 0.30$, the second number is the 95% CI). In addition, the removal of cranberry runners (P+R-) and the removal of plants (P-R+) resulted in two significantly different plant communities ($\Delta \text{NMDS1}=0.52 \pm 0.27$). Also, as shown in Figure 4 (b), the species composition under *Carex* was different compared to under cranberry runner ($\Delta \text{NMDS2}=0.29 \pm 0.20$), while the species composition under *Lachnanthes* is marginally different from under runner ($\Delta \text{NMDS2}=0.18 \pm 0.19$), but not from under *Carex*.

4. DISCUSSION

This study demonstrated that despite over 70 years of cranberry cultivation, viable seed banks of native wetland species remain in the agricultural soil profile. However, the past agricultural activities do have a legacy effect on the germination from these seed banks. The density and community composition of the seed bank in the original wetland soil (i.e. the bottom layer) is very different from the seed bank created during and after agricultural activities (i.e. the middle and top layer). Moreover, the plants germinated from the seed bank are strongly affected by the hydrology of the bogs and the existing vegetation on the bog surface. My result also demonstrated that flooding treatments commonly used in restoring other types of wetlands have surprisingly little effect on plant establishment from the seed bank. Rather, manipulation of the surface vegetation and the manipulation of soil layers will have greater effects on the community establishment from the seed banks.

Together, these results suggest that in an abandoned wetland farm, the

heterogeneous post-abandonment habitat conditions (i.e. bog hydrology and soil strata) are important factors to determine the seed bank's viability and the density of recruiting seedlings. Bog hydrology significantly changed the overall probability of viable seeds being present. In fact, only half of soils from the dry bogs exhibited germination (56.3%), which was significantly lower than the wet bogs. In addition, the bottom layer showed significantly lower probability of germination presence than the top and middle layers, especially in the bottom layer of dry bogs (Figure 1a). Out of the 16 trays obtained from bottom layer of the dry bogs, only 2 trays (12.5%) showed germination. This low occurrence is speculated to be due to the sandy soil texture underneath the dry bogs. Compared with wet bogs, dry bogs are more typically found farther from the upstream reservoirs, in the transition zone from wetland to upland. Roman *et al.* (1985) demonstrated in the Pinelands, soil typically changes from Muck (high organic content) to Atsion series (high sand content) as wetland transitions to upland. Therefore, soils from the bottom layer of dry bogs are characterized by higher sand content. This texture and organic matter difference probably caused the difference in seed bank's viability during the years of cranberry cultivation, which therefore changed the current seed bank's germination probability.

Compared to the probability of germination, the germination density exhibited a different pattern. Seedlings germinating from dry bogs were denser than from wet bogs (Figure 1b). As discussed above, only very few trays from the dry bog's bottom layer showed germination, indicating the high seedling density in dry bogs is driven by their middle and top layers. On the other hand, the higher overall germination density from the bottom layer than the middle and top layer (Figure 1b) is driven by the bottom layer of

wet bogs. These results suggested that we should apply different restoration strategies in the wet and dry bogs in order to best achieve the restoration goals. Although previous studies have suggested that removing top soil in disturbed wetlands can be applied to reduce agricultural weed or invasive species (Bakker *et al.* 2005; Hausman *et al.* 2007; Verhagen *et al.* 2001), my findings suggested this method cannot be applied in all bogs. In the wet bogs, the removal of top and middle soils will expose the high density seed bank in the bottom soil. However, in the dry bogs, viable seeds are mainly contained in the top and middle layers. The NMDS analysis further suggested seed banks from dry and wet bogs will result in different plant communities. Plant community from the wet bog's bottom layer is composed mainly of the local wetland species (Figure 2b). But the dry bogs did not correspond to any specific plant communities. My study showed that the agricultural activities can further increase the habitat heterogeneity that existed before the construction of farmlands. This heterogeneity will strongly affect the outcome of restoration, if the seed bank is used as the main source of vegetation development during restoration. Therefore, different restoration aims and approaches should be applied for the wet and dry bogs, instead of applying the same strategy across the landscape.

In comparison to the soil depth and bog hydrology, flooding treatment did not create as significant effects on the species composition of the germinated wetland community. Neither did flooding change the germination probability. Therefore for restoration purpose, flooding can be applied as a means to stimulate germination only if viable seeds are present (Fig. 1). It is critical then for us to conduct preliminary study to detect the seed viability before applying flooding as a restoration method to the entire targeted landscape.

Compared with the heterogeneity caused by different post-agricultural abiotic conditions, the biotic legacy in the abandoned farms can be significantly modified by the removal of ground cover species and woody cranberry mats. The DIC of candidate models clearly demonstrated that the removal of ground cover is a more important factor to explain the variance of germination densities than the existing vegetation (i.e. *Carex*, *Lachnanthes* or runner). Removal of either the dominant plant or of cranberry residues increased the germination, but the removal of both did not create further increase (Figure 3b). The comparison of overall germination density under the three cover types suggested that redroot (*Lachnanthes caroliniana*) caused a weak but significant decrease of germination compared with soils with only cranberry residue (Figure 3a). Plants of the genus *Lachnanthes* can secrete bioactive chemicals from their roots (Neori *et al.* 2000), which suggests possible allelopathic functions that can reduce the germination of other species. Since my removal treatment only involved the aboveground tissue, I was not able to test whether the removal of this plant's rhizome can further trigger more germination.

I was able to show that the ground cover removal treatment will expedite the initial process of post-abandonment succession across different plant community types by increasing germination density. In contrast, the existing abiotic differences created stronger barriers to hydrological restoration treatments (i.e. the flooding treatment). Although flooding is an effective way to change the growth and survivorship of various wetland species in natural wetlands (Miller and Zedler 2003), the soil seed bank composition and viability in abandoned wetland farms had been greatly altered by human agricultural activity. The bogs' water table and soil profiles played a bigger role in

determining the germination probability and density. The results suggest that scientists and restoration practitioners must consider the altered habitat conditions while enacting restoration strategies in a human modified habitat, rather than applying the same practice across the landscape. Although the existence of viable native seed banks suggests that natural succession is a promising force for restoration, we cannot assume that succession will happen homogeneously. The plant community in some regions can become dominated by weed or non-native species because of the agriculture's legacy effect. Some modified habitat conditions may have long-term effects on restoration even decades or possibly centuries after termination of human activities. Ignoring these long-term influences may reduce restoration efficiency, or produce undesirable results.

Implications for Practice

1. The remaining seed bank in human disturbed habitat can exhibit great variability across the landscape. Therefore, if the seed bank is used as the main propagule source for restoration, pre-sampling of the seed bank's composition and viability across the landscape is necessary in an agriculturally modified habitat. In areas where seed bank in deeper soil is still viable and contains seeds from the original plant communities, top soil removal can be an effective method for restoration. But in other areas, addition of seed sources is necessary to reduce the dominance of weed communities that remains in the seed bank.
2. Flooding can increase the germination density in restored wetland only if there are viable wetland vegetation seeds present in the soil.
3. Removal of agricultural remnant plant tissue can significantly increase the germination density from the seed bank.

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Table1. Factorial design of ground cover types and removal treatments. “+” indicates presence, “-“ indicates removal; P_c —*Carex*, P_L —*Lachnanthes*, R—runner. The design resembles a two-way ANOVA that the effect of the removal treatment, the ground cover types and their interactions is modeled by parameter β_{cover} , β_{rmvl} and $\beta_{\text{cover*rmvl}}$ in the Bayesian Generalized Linear Model.

Removal treatments	Ground cover types		
	Runner (n=4)	<i>Carex</i> (n=4)	<i>Lachnanthes</i> (n=4)
a. Original ground cover (control)	R+	P_c +R+	P_L +R+
b. Runner removal (leaving the plants)	R-	P_c +R-	P_L +R-
c. Plant removal (leaving the runners)	————	P_c -R+	P_L -R+
d. Both runner and plant removal	————	P_c -R-	P_L -R-
e. Both runner and plant removal; loosened surface soil	Loose	Loose _c	Loose _L

Table 2. DIC of candidate models. In each model, the effect of ground cover types, the effect of removal and their interaction is parameterized by β_{cover} , β_{rmvl} and $\beta_{\text{cover*rmvl}}$, respectively. (Refer to Table 1 for details of each factor). The tope mode is the one with the lowest DIC value. Δ DIC indicates the difference of the DIC value between the tope model and each candidate model.

Label	Description:	Formula:	DIC	Δ DIC
1	No interaction	$\mu = \beta_{\text{cover}} + \beta_{\text{rmvl}}$	23. 862	0
2	Removal treatment effect	$\mu = \beta_{\text{rmvl}}$	25. 666	1. 8
3	Full Model	$\mu = \beta_{\text{cover}} + \beta_{\text{rmvl}} + \beta_{\text{cover*rmvl}}$	27. 918	4. 056
4	Ground cover effect	$\mu = \beta_{\text{cover}}$	35. 421	11. 559

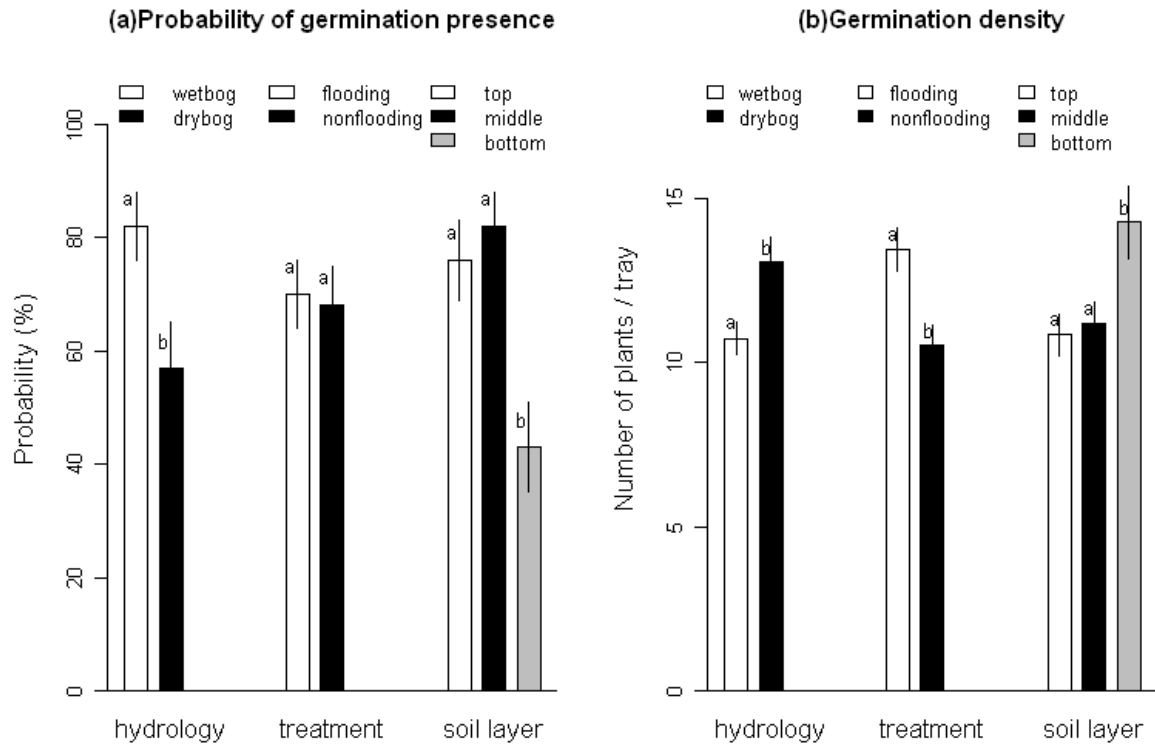


Figure 1. The comparison of (a) the probability of germination presence and (b) germination density of wet vs. dry bogs, flooding vs. non-flooding treatment, and top vs. middle vs. bottom layer. As stated in section 2.3.2, the probability of germination presence (a) was modeled by the binomial distribution in the ZIP model, and the germination density (b) was modeled by the Poisson distribution. Bars represent mean probability or density \pm Standard Deviation. Letters indicate significant differences among values, namely, different letters indicate that the difference's 95% credible interval (CI) does not overlap 0.

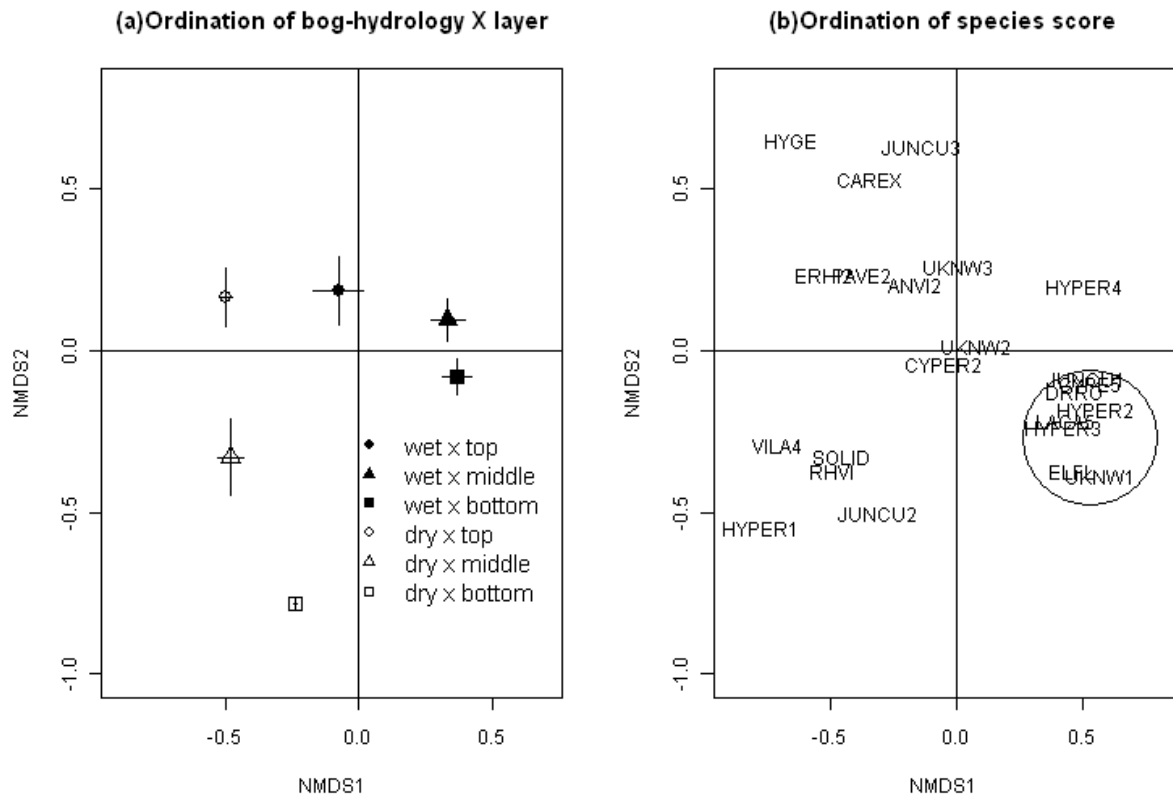


Figure 2: Ordination of species composition from each bog hydrology x layer. (a) Ordination of top, middle and bottom layer in wet and dry bogs. For simplicity, rather than the germination result of all 69 trays, each bog hydrology x layer combination is plotted with its mean value along axis 1 and 2. The error bars indicate \pm SE. (b) Ordination of plant species along NMDS 1 and 2. The species cluster within the oval shape corresponds to the wet x bottom ordination in graph (a).

Species names: HYGE—*Hypericum gentianoides*; JUNCU3 — *Juncus sp.3*; CAREX — *Carex sp.*; ERHI2 — *Erechtites hieracifolia*; PAVE2 — *Panicum verrucosum*; UKNW3 — Unidentifiable sp. 3(dicot); ANVI2 — *Andropogon virginicus*; HYPER4 — *Hypericum sp. 4*; UKNW2 — Unidentifiable sp. 2 (monocot); CYPER2 — *Cyperus sp.2*;

VILA4 — *Viola lanceolata*; SOLID — *Solidago sp.*; RHVI — *Rhexia virginica*;
HYPER1 — *Hypericum sp. 1*; JUNCU2 — *Juncus sp. 2*.

Species within the cluster: ELFL — *Eleocharis flavescens var. olivacea*; CYPE5 —
Cyperus retrorsus; JUNCU1 — *Juncus sp. 1*; DRRO — *Drosera rotundifolia*; HYPER2
— *Hypericum sp. 2*; LACA5 — *Lachnanthes caroliana*; UKNW1 — Unidentifiable sp. 1
(dicot); HYPER3 — *Hypericum sp. 3*

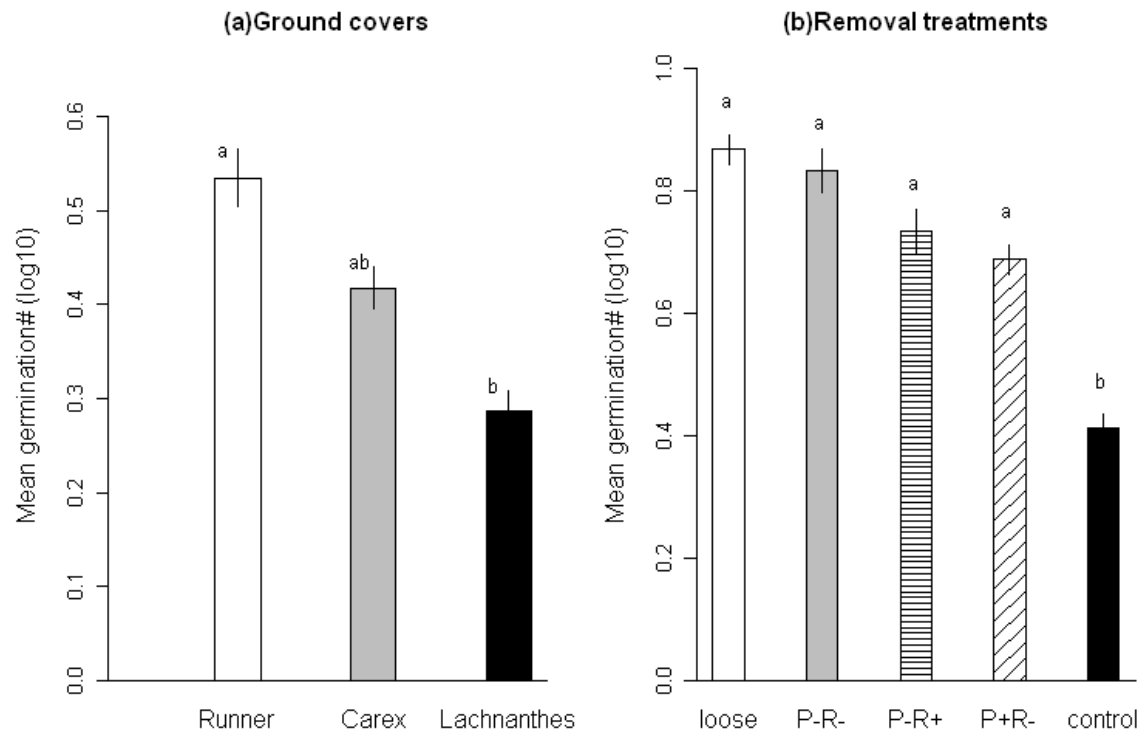


Figure 3: Mean germination (a) under ground cover — Runner, *Carex* and *Lachnanthes*; (b) under different removal treatments (as shown in Table1). Because the analysis result indicated that the interaction between the two factors was not important to explain the variation of germination (3.2.1), the removal treatments in Table 1 were clumped across all three ground cover types (as Loose, P-R+, P+R-, P-R- and control). Error bars indicate \pm standard error.

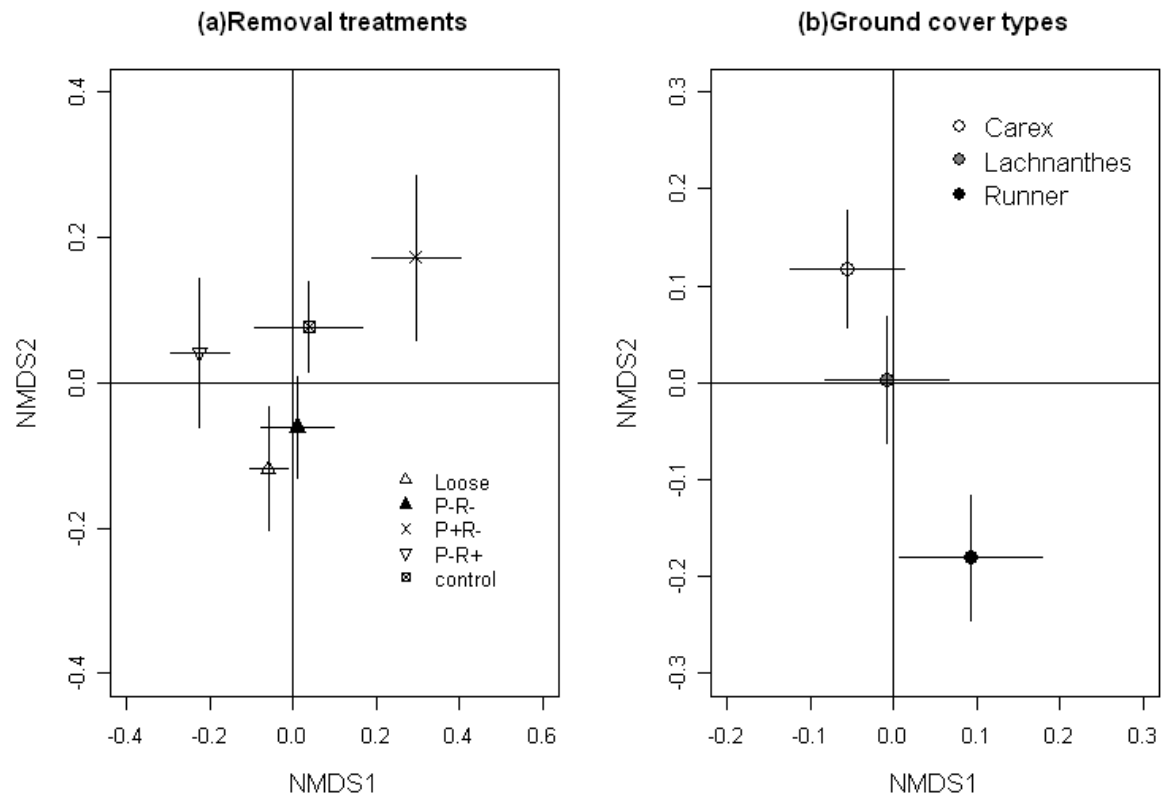


Figure 4. Ordination of removal and ground cover types along NMDS axes 1 and 2. The average NMDS1 and NMDS2 value of each removal and ground cover type is shown with error bar indicating \pm SE. (a) The P-R+ and P+R- treatments are significantly separated from other removal treatments along the first NMDS axis. (b) The species composition from trays covered by *Carex* and *Lachnanthes* is significantly separated by NMDS2.

APPENDIX 1: Species list and abundance of experiment 1

species	common name	ABRV	number
<i>Erechtites hieracifolia</i>	fireweed	ERHI2	3
<i>Solidago sp.</i>		SOLID	4
<i>Panicum verrucosum</i>	warty grass	PAVE2	5
<i>Hypericum canadense</i>	Canada St. Johnswort C	HYPER4	5
<i>Juncus sp. 3</i>		JUNCU3	5
<i>Hypericum gentianoides</i>	orange grass	HYGE	6
<i>unknown dicot 1</i>		UKNW1	9
<i>Viola lanceolata</i>	lance-leaved violet	VILA4	10
<i>Hypericum sp. 3</i>		HYPER3	12
<i>Lachnanthes caroliana</i>	redroot	LACA5	14
<i>unknown monocot</i>		UKNW2	17
<i>Cyperus sp.</i>		CYPER2	19
<i>unknown dicot 2</i>		UKNW3	19
<i>Drosera rotundifolia</i>	roundleaf sundew	DRRO	20
<i>Cyperus retrorsus</i>	nutsedge	CYPE5	23
<i>Andropogon virginicus</i>	broomsedge	ANVI2	48
<i>Hypericum sp. 2</i>		HYPER2	49
<i>Hypericum sp. 1</i>		HYPER1	52
<i>Eleocharis flavescens var. olivacea</i>	spike rush	ELFL	55
<i>Carex sp.</i>	three-way sedge	CAREX	64
<i>Juncus sp. 2</i>	rush	JUNCU2	98
<i>Rhexia virginica</i>	meadow beauty	RHVI	146
<i>Juncus sp. 1</i>	rush	JUNCU1	394

Appendix 2: Species list and abundance of experiment 2

species	common name	ABRV	number
<i>Carex sp. 2</i>	three way sedge	CAREX	0
<i>Unknown monocot 1</i>		UNKN	1
<i>Unknown Fabaceae</i>		FABA	1
<i>Panicum verrucosum</i>	warty grass	PAVE2	2
<i>Digitaria sanguinalis</i>	crabgrass	DISA	2
<i>Juncus sp. 3</i>		JUNCU3	4
<i>Amphicarpum amphicarpon</i>	double millet	AMPU6	5
<i>Juncus sp. 2</i>	rush	JUNCU2	5
<i>Hypericum sp.</i>	St. Johnswort	HYPER	7
<i>Panicum sp.</i>		PANIC	10
<i>Erechtites hieracifolia</i>	fireweed	ERHI2	15
<i>Lachnanthes caroliana</i>	redroot	LACA5	17
<i>Carex striata</i>	three way sedge	CAST41	21
<i>Unknown monocot. 2</i>		ANDRO2	36
<i>Juncus sp. 1</i>	rush	JUNCU1	39
<i>Andropogon virginicus</i>	broomsedge	ANVI2	116

CHAPTER 3

Vegetation structural and anuran community dynamics in post-agricultural wetlands: post initial establishment stage

ABSTRACT

Wetland succession has been studied under field and experimental conditions, but little has been done to examine the chronological development of wetlands under different hydrological conditions. In reality, community dynamics in wetlands rarely follow a successional trajectory without the interference of changing hydrological conditions, especially if the wetland has been disturbed by human activities. I studied the vegetation and anuran community development in different-aged abandoned cranberry farms, which is a unique system that allows us to examine wetland dynamics over time and across a hydrological gradient. The study demonstrated that the wetland coverage and height increased linearly as habitats were located farther downstream from the water source, indicating that hydrology plays a major role in determining the pace of vegetation development. In comparison, time did not contribute to the variance of the vegetation structure variables, even though there are decades of difference in the farms' abandonment histories. In addition, anuran richness decreased significantly from upstream to downstream in the wetland series. The densities of two anuran species, *Rana (Lithobates) virgatipes* and *Rana sphenoccephala*, were negatively correlated to increased vegetation coverage and height, indicative of these species' preference of open water during breeding season. Finally, I discussed the importance of a diverse vegetation structure to maintaining anuran species richness during the succession of natural or disturbed wetlands.

INTRODUCTION

Around the world, many wetlands have been converted into agricultural lands with the subsequent loss of important ecosystem functions (Wheeler *et al.* 1995; Yamada *et al.* 2007). After the agricultural activities are terminated, wetland function can be recovered if suitable vegetation and animal communities can be re-established. In order to understand the influence of agriculture on wetland, many studies have been conducted to investigate species dynamics in these human-modified wetlands. Although studies using an archaeological approach have shown that the effects of historical agricultural activities on wetland communities can last over the time frame of centuries to millennia (Ellis and Tallis 2000; Beach *et al.* 2008), the majority of research efforts have been investigated on short-term (<20 years) community recruitment because of its importance for restoration (Comin *et al.* 2001; Battaglia *et al.* 2002; Mazerolle *et al.* 2006; Hausman *et al.* 2007). Relatively fewer studies were aimed at examining the post-agricultural wetland dynamics beyond the initial recruitment period. Observations of succession over 15-20 years are rare (Foster & Tilman 2000) because of the difficulties in continuous long-term observation. The majority of the few established long-term ecological research (LTER) cases are in upland post-agricultural systems (Foster & Tilman 2000; Pickett 2001).

Meanwhile, even fewer studies have addressed the changes in animal communities beyond the initial animal recruitment period. Animal communities such as anurans are important elements in wetland food webs (Altig *et al.* 2007; Schiesari *et al.* 2009). Tadpoles and adult anurans consume a variety of vegetative and animal food; they also serve as prey for many predators at different tropical levels. Maintaining an abundant and stable anuran community is therefore critical for the integrity of a wetland's food-web

and its ecological function. Anuran metacommunity's dynamics among ponds with different environmental conditions have been studied by Werner et al. (2007a; 2007b; 2009). They provided strong evidence that during a decade time-span, anuran larval diversity was positively correlated with the pond's hydroperiod and size, while negatively correlated with canopy cover. These findings concurred with other studies that demonstrated the importance of vegetation structure on the survival of anuran larvae and adults (Skelly et al. 1999; 2002). Although, in these studies, the targeted wetlands' vegetation and hydrological features were mostly treated as static factors (except Werner 2009). We still lack information about the changes of amphibian communities over a longer time span in respond to the chronological development of the vegetation structure. More importantly, we need to understand how human agricultural activities have modified wetland succession, and how long the anthropogenic influences will persist.

In this study, I examined changes in vegetation structure and anuran community composition along human modified hydrological gradients during later stage of succession. I explicitly inspected the chronological development of vegetation structures and anuran communities, as well as their correlation with the modified hydrology in post-agricultural habitats. The study was conducted in different-aged cranberry farms in the Pinelands of New Jersey. Cranberry (*Vaccinium macrocarpon* L.) is a native wetland species indigenous to the Pinelands. The commercial cranberry crop was cultivated by constructing cranberry farms in wetlands along streams and rivers, usually on hydric mineral soils (Markley 1998). Cranberry farms constructed before the mid-20th century comprised a sequence of cultivation beds along the stream channel. The cultivation beds were excavated to be lower than the ground along stream channels (hereafter "bogs";

Figure 1). Between connected bogs, dams were built to control water flow. The most upstream section was usually constructed with a raised water level (hereafter “reservoir”) to provide a supply of water for the downstream bogs (Procopio and Bunnell 2008). After farm abandonment, human’s active management of the dams was also terminated, which allowed some natural water flow across the sequence of bogs to resume. Because the hydrology of the most downstream bog unit then depends on the extent and pattern of water discharge in the upstream bogs as well as the reservoir, the series of bogs along a riverine corridor develops a gradient of hydrologic conditions. Visual observation suggests that bogs close to the reservoir are wetter than the bogs farther downstream (Figure 1), depending on their proximity to the reservoir and the pattern of dike and dam decay. On the maps provided by U.S. Fish & Wildlife Service, the bogs from upstream to downstream within these farms are typically classified in a hydrological sere, such as lake (usually the reservoir), to freshwater pond, to freshwater emergent wetland, to freshwater forested/shrub wetland as the most downstream bog (U.S. Fish & Wildlife Service 2010). Thus, by using the LiDar technique, I can quantitatively examine the changing of vegetation structural along the bog sequence and relate the anuran community composition with the development of vegetation structures. I can then reveal the effect of post-agricultural hydrology on the re-establishment of the freshwater flora and fauna.

I conducted the study in abandoned cranberry farms that are aged 50 to 80 years after farmland abandonment. Wetlands at this age likely have gone beyond the initial “seed spreading” stage of plant colonization and new species recruitment rate is much lower than the first decade after abandonment (van der Valk 1992; Lee *et al.* 2002; Lu *et al.* 2007). I was interested in examining whether the vegetation structure still undergoes

chronological changing in wetlands at this post-agricultural stage, and whether the anuran communities also exhibit chronological changes as a response. Thus, using the different aged cranberry farms, I could apply a space-for-time approach (a.k.a. static approach, Pickett 1988; Foster and Tilman 2000) to study the effect of age on post-agriculture vegetation structure change. Johnson and Miyanishi (2008) argued that this approach requires a rigid assumption that all sites must have the same initial conditions. They pointed out that this assumption has been neglected in many previous space-for-time studies. In our study, all the abandoned cranberry farms started as palustrine fields covered with cranberry woody tissues without other above ground vegetation structure. I can therefore limit the “initial condition” assumptions that confound other space-for-time approaches. By comparing models with or without “farm” as a factor, I can determine whether the vegetation structure and animal composition has a significant variation among farms, which will indicate the effect of age.

I hypothesized that the characteristics of vegetation structure in bogs within the same farm should exhibit a linear relationship along the bog sequence, reflecting distance from the reservoir. Second, I hypothesized that vegetation structure should exhibit significant among-farm variation, reflecting age since abandonment. If only age, and not a hydrological legacy, controls succession development, I would expect newly abandoned farms to have less vegetation cover and lower heights than older ones, on which more advanced forest development should be observed. If hydrological legacy is important, I would expect that age alone does not predict vegetation structure. Last, I hypothesized that anuran species that need open water during breeding seasons of their lifecycles will demonstrate a stronger response to the hydrology effect than habitat generalists. Based on

the documented negative correlation between canopy cover and anuran larval survival (Werner et al. 2007a), I expected a negative relationship between the vegetation coverage and the density of anurans.

METHODS

Study sites:

This study was conducted in eight abandoned cranberry farms in the Mullica River Basin and Rancocas Creek Basin in the Pinelands of southern New Jersey. These cranberry farms were constructed in wetlands that bordered stream channels (Procopio and Bunnell 2008). Pinelands streams are characterized by low topographic gradients, high acidity, low concentrations of dissolved organic matter, and slow water flow (Patrick et al. 1998). Cranberry farms were typically constructed over muck and peat soils, which were originally covered with cedar swamps and hardwood swamps (Ehrenfeld 1986; Procopio and Bunnell 2008). The common canopy species include Atlantic white cedar (*Chamaecyparis thyoides*), red maple (*Acer rubrum*), black gum (*Nyssa sylvatica*), pitch pine (*Pinus rigida*), gray birch (*Betula populifolia*) and sassafras (*Sassafras albidum*). The understory is comprised of highbush blueberry (*Vaccinium corymbosum*), leatherleaf (*Chamaedaphne calyculata*), dangleberry (*Gaylussacia frondosa*), sheep laurel (*Kalmia angustifolia*), staggerbush (*Lyonia mariana*) and other shrub species. Leatherleaf, together with some other shrubs, often grows into the stream channels to form dense thickets. The herbaceous community is made up of various sedges (*Carex spp.*), rushes (*Juncus spp.*) and dense peat mosses (*Sphagnum spp.*). These herbaceous species grow along the margins of stream channels, surrounding and beneath the band of shrub thickets.

The native cranberry also typically grows along stream edges (Eck 1990).

American cranberry has been cultivated in this area since the mid-19th century (Zampella *et al.* 2006). The current cranberry acreage is only one-third of the acreage that existed at the peak cultivation time in the early 20th century. The abandoned cranberry farms are scattered in the Pinelands landscape, and many of them are difficult to access due to poor road conditions after decades of neglect. In addition, the history of many abandoned farms is hard to trace if the farmers have left the area. Therefore, I interviewed local farmers and residents to help us choose eight farms based on their accessibility and relatively clear time (estimated to the decade) of abandonment. The names of the farms and their abandonment histories are listed in Table 1.

Vegetation variables:

Wetland vegetation structure was measured using the LiDAR (Light Detection and Ranging) technique. LiDAR is an effective tool to detect vegetation height and has been applied to detect forest structures and community composition (Hurt et al. 2004; Skowronski et al. 2007). It has also been applied recently to examine forest succession (Falkowski et al. 2009), because the vegetation height is expected to follow a certain pattern during succession.

The LiDAR acquisition covered the entirety of Burlington and Camden counties in New Jersey. The acquisition was flown at an altitude of 5,500 ft. above ground level during leaf-on conditions from October 1st to October 7th, 2004 by Airborne 1 Corporation. The data was acquired using an Optech ALTM 2050 with first and last returns being digitized with an average ground spacing of ca. 1 pulse/m². Horizontal and vertical accuracies of the LiDAR returns were reported as being better than 0.3 meters.

This data is available publicly on the USGS CLICK website (<http://lidar.cr.usgs.gov>).

For this study, the LiDAR data was spatially subset by visually-digitized polygons of the extent of the farms described above. Farm 60F1 was located outside of Burlington and Camden counties and therefore was not included in the vegetation coverage analysis. This resulted in 30 individual LiDAR point clouds, attributed by individual bog. I used the Toolbox for LiDAR Data Filtering and Forest Studies (TiFFS) software (Chen 2007) to develop a digital elevation model (DEM), a digital surface model (DSM), and a canopy height model (CHM) for each bog. The CHM model was then used to generate a 1m-resolution vegetation height map for each bog by averaging the canopy height within each 1m*1m pixel of each bog.

The vegetation heights from the 1m-resolution layer were rounded to the closest integer. The number of pixels with the same height (hereafter as “bin”) was used to construct the vegetation height histogram of the bog. Because returns with less than 0.5m can result from noise generated from the creation of the reference ground spine, pixels with <0.5m were rounded to 0m and were considered as no vegetation coverage (a.k.a. No Veg; see discussion). Pixels with exceptionally large height return can also be due to noise (i.e. these pixels are actually located around the bog rather than within the bog). Therefore, within each bog, bins containing pixels that cover less than 1% of the total bog area were removed. The bog’s histogram was then used to extract the bog’s vegetation variables. The variables include vegetation percent coverage ($[\text{total area} - \text{No Veg}] / \text{total area}$); maximum vegetation height in the bog; median of the histogram; skewness of the histogram; and mean vegetation height weighed by number of pixels in each bin as formula.

$$\text{weighed mean vegetation height} = \frac{\sum_{\text{height}=1}^{\text{max height}} \# \text{ of pixels} * \text{height}}{\text{total} \# \text{ of pixels}}$$

Anuran vocal survey:

I conducted anuran nighttime vocalization surveys from April through July in 2008. Because of very poor accessibility during June-July, farms 40F1 and 50F3 were not surveyed for anurans and were excluded in anuran-related analyses (Table 1). The other farms were visited at least twice a month. Within each farm, each bog was surveyed from 2-4 fixed locations on surrounding dikes. The locations were selected to be accessible by foot and to maximize the distance from other bogs in order to ensure independence of the surveys. Each survey took place between sunset and midnight. During each visit, I scored the maximum number of vocalizing individuals of each anuran species during five minutes according to the following categories: 1 (1 individual), 2 (2-5 individuals), 3 (6-10 individuals) and 4 (more than 10 individuals) (modified from Heyer *et al.* 1994). The calling intensity was recorded for each species at the specific location during each visit. At the end of the season, each species' calling intensity from all surveys was averaged across all survey locations for each specific bog.

Statistical Analyses:

I applied linear regression with a non-parametric randomization test (Crowley 1992) to test whether the dependant variables (i.e. vegetation variables and anuran density/diversity) changed linearly along the bog series within the farms. Because the anuran survey and the LiDAR analysis was conducted using each bog as a unit, the bog's order in the queue of bogs within each farm was used as its relative distance from the upstream reservoir. For example, if the farm had five bogs, the bog closest to the

reservoir was assigned as 1, while the farthest bog was assigned as 5. Thus, if the measured dependant variable exhibited linear change along the bog sequence, the t-statistics of the regression would be significant ($p_{\text{bog}} < 0.05$).

Because the rank-based anuran data and the LiDAR derived vegetation variables violated the assumption of normality in the normal-theory linear regression, I could not use the t-distribution to test the null-hypothesis. Instead, I applied data randomization to generate the distribution of the linear regression's t-value by recording the t-value after each permutation. After 3000 permutations, the generated distribution was used to determine whether the observed t-value was located within the 95% confidence interval. If the observed t-value was within the confidence interval, it indicated that the observed pattern of dependant variables (i.e. anuran density or vegetation variables) was not different from a pattern that was drawn randomly; otherwise, if the t-value was within the tail of the generated distribution, it indicated that the observed dependant variables exhibited significant correlation with the bog sequence. The sign of the t-value indicated whether the dependant variable increased (+) or decreased (-) for bogs that were sequentially located farther from the reservoir. To detect the variation of variables among different farms, I conducted a Likelihood Ratio Test (Pinheiro and Bates 2000) of models with and without farm as a random effect. The returned p-value from the Likelihood Ratio Test (p_{farm}) was used to determine whether including farm effect could increase the fitness of the model to predict the dependant variable, which would suggest that the among-farm differences accounted for the variation of the observed dependant variable.

I also examined the correlations between two anuran variables (i.e. density and diversity) and two vegetation variables (vegetation coverage and mean vegetation height),

regardless of bog location in the farms. I used a non-parametric test similar to that described above to generate the t-distribution by randomizing the vegetation variables within each farm for 3000 permutations. The correlations between anuran and vegetation variables were determined based on whether the observed t-values were located within the confidence interval of the generated distribution. The analyses were conducted using the program R (2.8.0).

RESULTS

Vegetation features along the bog sequence

Using the histograms of each bog's LiDAR return, I identified three prominent successional stages of the bogs: an early stage represented by histograms with excessive "zero" returns; an intermediate stage with histograms that were less skewed compared with the early stage; and a late stage characterized by histograms that approach a normal distribution (Figure 2).

The analysis of the variation of vegetation variables along the bog sequence and among different farms is shown in Table 2. The likelihood ratio test showed that regression with "farm" as a random effect was strongly preferred compared to the regression without it for all the vegetation variables ($p_{\text{farm}} < 0.05$ for all variables). Only the median height of the pixels showed significant increase as the bogs were located farther from the reservoir (median $p_{\text{bog}} = 0.0137$). However, examination of the plotted data showed that variables of farm 40F1 were distinctively different from those of other farms (e.g. Figure 3(a) shows that the vegetation coverage of 40F1 was different from that of the other farms). I suspected that the significant variation among farms was largely driven by this single farm. In order to remove the possible bias caused by this single farm,

I conducted another regression analysis without farm 40F1. No variables differed among farms when farm 40F1 was excluded. Instead, the bog sequence was shown to have a significant effect on the median vegetation height as well as the bog's vegetation coverage (Table 2, 6 farms). As shown in Figure 2(b), the vegetation coverage significantly increased as the bogs were located farther away from the reservoir ($p_{\text{bog}}=0.042$).

Anurans' distribution along the bog sequence

Eight species of anurans were observed in the six farms (Table 2). Four species, spring peeper (*Pseudacris crucifer*), carpenter frog (*Rana (Lithobates) virgatipes*), southern leopard frog (*Rana sphenoccephala*) and green frog (*R. clamitans*), were distributed in at least five out of the six farms. Therefore, the density of these species was analyzed against the bog sequence. The other four species, Pinelands treefrog (*Hyla andersonii*), northern grey treefrog (*H. versicolor*), Fowler's toad (*Bufo fowleri*) and bullfrog (*Rana (Lithobates) catesbeiana*), were distributed in fewer than five farms. These species were included in measurement of anuran species richness, but their density was not analyzed as individual species.

The randomization analysis showed that the total species richness exhibited a significant decrease along the bog gradient from upstream to downstream (Table 3, Figure 4; observed $t = -2.439$, $p = 0.023$). But the species richness did not differ significantly among different farms ($p_{\text{farm}} = 0.999$). One species, the carpenter frog, significantly decreased in density in bogs farther from the reservoir (Table 3; observed $t = -2.244$, $p = 0.035$). In addition, two species exhibited significant density variation among farms (Table 3, green frog $p = 0.036$; carpenter frog $p = 0.021$).

Correlation between anuran distribution and vegetation features

The correlations among anuran density and diversity and the two vegetation variables (coverage and average height) are summarized in Table 4. None of the regressions exhibited significant variation among farms. The densities of two frog species, the carpenter frog ($t_{\text{bog}} = -2.15$) and the southern leopard frog ($t_{\text{bog}} = -2.56$), exhibited significant negative correlation with the vegetation coverage in the bogs (Table 4). The southern leopard frog's density ($t_{\text{bog}} = -2.076$) also showed a significant negative correlation with the bog's average vegetation height (Table 4).

DISCUSSION

Our study demonstrated that the development of vegetation structure within abandoned cranberry bogs in the post-agriculture wetlands is largely determined by the location of each bog within the farm, which is along an apparent hydrological gradient. Although the farms had decades of difference in their abandonment histories, the models that include both farm and bog sequence as explanatory factors were not significantly superior to the model with only bog sequence, which suggested that farm did not contribute significantly to the variation of vegetation structure, with the exception of one farm. The bog sequence and the vegetation structure had further influenced some aspects of anuran species' distributions, demonstrated by the decreased species richness from up- to downstream along the bog sequence. Two species, the carpenter frog and the southern Leopard frog, had explicitly exhibited reduced density as the bog's vegetation coverage increased. This research demonstrated that in these wetlands, human modified hydrology had a prolonged influence on the wetland's vegetation and animal communities for

decades after the cessation of human activities.

The LiDAR method successfully captured the structural changes of the vegetation in the cranberry farms. I was able to conceptually view the histogram of vegetation at different successional stages, as well as to mathematically extract structural variables from the histograms to compare the vegetation development in different bogs. LiDAR methodology does have technical limitations when applied in wetland systems. The method used to generate ground surface caused background noise which resulted in low reliability of returns less than 0.5m high (Skowronski et al. 2007). In addition, I used the commonly applied infra-red light lasers to acquire LiDAR data, whose energy is absorbed by water (Julian *et al.* 2009). These limitations of LiDAR technology gave us limited ability to detect vegetation such as sphagnum mosses and low herbaceous species; neither could I determine whether the vegetation was located in standing water or on the ground. To resolve this problem, I binned all returns less than 0.5m with 0m return and treated the pixels as “no vegetation”. This resolution reduced our ability to detect coverage of low vegetation. However, our goal was to detect the vegetation structural development in different-aged farms. I treated each individual bog as a unit to compare the changing of the vegetation height profile. Therefore, the bias in our method was consistent across all units and did not influence our comparison of the histogram characters among different farms. If our goal were to trace the changing of low vegetation across hydrology and time, I would need to use satellite images with LiDAR information to better detect and classify areas with low vegetation and water (Maxa and Bolstad 2009).

The regression analysis indicated that the current vegetation’s median height and total coverage was significantly correlated with bog location within the farm (Table 2, 6

farms). This is likely due to the gradient of hydrological conditions created by the series of dams within each farm. The effect of dams on water-flow, water table and vegetation growth has been well studied (reviewed by Heppner & Loague 2008). Dams can reduce the downstream streamflow (Constantz 2003), reduce peak discharge (Gordon & Meentemeyer 2006), and increase the downstream channel incision as well as riparian plant coverage (Ligon et al. 1995; Gordon & Meentemeyer 2006). Therefore, I believed that the series of dams in each farm had created a gradual sequence of habitat hydrology in the consecutive bogs, which resulted in the observed gradual changing of the vegetation's median height and vegetation coverage within the bog (Table 2, Figure 3). However, in farms 50F1, 50F3 and 60F2, several dams were damaged, probably due to age or human activities. In addition, there was evidence of beaver activity in several farms; beavers can create off-bank ditches and impoundments along the stream channels (e.g. in the aerial-photo in Figure 1, the bog next to bog4 has been permanently flooded due to beaver dams; it was not included in the study). I suspect that beaver activities have changed the hydrologic features in these bogs and consequently caused temporary or long-term variation of the development of riparian vegetation (Westbrook 2006). This probably caused the noise in the regression of the vegetation variables, although the vegetation's median height and coverage still exhibited a significantly increasing trend as the bog is located farther from the reservoir.

Compared to the linear nature of the within-farm variation of the vegetation characters, the among-farm variation was more case-specific. The significance of the variation was determined by whether farm 40F1 was included in the analysis (Table 2). When the analysis included this farm, the among-farm variation significantly increased

the fit of the regression model (likelihood ratio test $p_{\text{farm}} < 0.05$), which indicated that there was significant among-farm variation of vegetation characters. However, without farm 40F1, the variation among other farms did not contribute to the explanation of the overall vegetation variance, although these farms had decades of difference in their abandonment histories. A current aerial photograph shows that farm 40F1 has significantly denser vegetation than other farms. When plotted, all the vegetation variables of this farm were noticeably divergent from other farms (e.g. Figure 3a). Unfortunately, I have limited information regarding what human or natural activities have happened on this farm since abandonment. However, the aerial photo shows that farm 40F1 is the only one among our study sites that does not have a reservoir with visible standing water. I suspect that this farm's surrounding environment has been tremendously changed since abandonment, which has drastically changed its hydrologic features and consequently resulted in faster vegetation structural development. I conclude that the influence on vegetation development caused by the abandonment history is not as strong as the effect created by the variation in habitat hydrology.

Our study suggests that as vegetation coverage increases during wetland succession, a wetland can potentially become a less suitable breeding habitat for anuran species. Both anuran species richness and the density of carpenter frogs decreased significantly in bogs located farther from the reservoir (Table 3, Figure 4 and 5), where vegetation coverage and median height were higher (Table 2). I also tested the correlation between anuran density and vegetation variables. Even with possible under-estimation of submerged and emergent vegetation coverage because of the detection limit of the LiDAR technique, I found a negative correlation between carpenter and southern leopard frogs' densities with

vegetation variables (Table 4). I attribute this to these two species' requirement of acidic water and their preference for long hydro-period temporary ponds or permanent water (Gosner and Black 1957; Zampella and Bunnell 2000; Ryan and Winne 2001). Previous studies under experimental condition have also shown that the survivorship of leopard frogs (*R. pipiens*) is lower under closed canopies than open canopies (Werner and Glennemeier 1999; Skelly *et al.* 1999). Werner *et al.* (2007a) suggested that canopy development during succession will impact the survivorship of anuran tadpoles. Our study provided direct field observational data to demonstrate that the densities of carpenter and southern leopard frogs during the breeding season is negatively correlated with increased vegetation cover. I concluded that in the long run, the development of vegetation in a human-modified palustrine wetland can gradually reduce the breeding habitat suitability for some hydrology-sensitive anuran species.

However, our finding cannot eliminate the possibility that the developed vegetation can serve as shelters for anurans during other stages of their life-cycle. As demonstrated by Babbitt and Tanner (1997), increased submerged vegetation complexity can increase the survivorship of southern leopard frog tadpoles; Otto *et al.* (2007) have also shown that well-developed forests can serve as important over-wintering habitats for carpenter frogs. Our result, in conjunction with these previous findings, suggests that in order to establish a diverse anuran community in a restored wetland, the hydrology of the restored habitat needs to be managed to allow the development of vertical complexity in the vegetation, as well as to maintain permanent water bodies to fulfill the requirement of certain amphibians. In our study, neither the vegetation characters nor the anuran diversity and density exhibited chronological variation among different-aged farms. The

variation among different bogs was largely explained by bog location within the farms rather than by the farms themselves. Our findings reinforced the importance of hydrology to wetland community development in a human-modified system. The termination of human physical activities does not necessarily remove the long-term influence caused by habitat modification, especially hydrologic change, and the influence will not fade over time.

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Table 1. Site information and the presence/absence of anuran species. “Year” is the approximate abandonment year of the farm. “LiDAR” and “Frog” columns indicate whether the LiDAR data or frog data is available for each farm (Y—available; N—not available). “+” and “-” indicates the presence or absence of a specific species in each farm. PSCR = spring peeper; RAVI = carpenter frog; RASP = southern leopard frog; RACL = green frog; HYAN = Pine Barrens tree frog; HYVE = grey treefrog; BUWF = Fowler’s toad; RACA = bullfrog.

Farm	# Bogs	Year	LiDar	Frog	PSCR	RAVI	RASP	RACL	HYAN	HYVE	BUWF	RACA
30F1	3	1930	Y	Y	+	+	+	+	+	-	+	-
40F1	4	1940	Y	N	na	na	na	na	na	na	na	na
50F1	5	1950	Y	Y	-	+	+	+	+	-	+	-
50F2	3	1950	Y	Y	+	+	+	+	-	-	-	-
50F3	4	1950	Y	N	na	na	na	na	na	na	na	na
60F1	6	1960	N	Y	+	+	+	+	+	+	-	-
60F2	7	1960	Y	Y	+	+	+	+	-	-	+	+
60F3	4	1960	Y	Y	+	+	+	+	-	-	+	-

Table 2. Regression of vegetation variables against the bog's distance from the reservoir. p_{bog} indicates the significance of the slope, given the distribution obtained from the randomization of 3000 iterations. For variables with significant p_{bog} (<0.05), positive t value indicates the variable increases as the bog is located farther from the reservoir. p_{farm} indicates the significance of the likelihood ratio test of the model with and without the farm effect. $p_{\text{farm}} > 0.05$ indicates that the farm effect does not contribute significantly to the fit of the regression. * indicates significant p value (<0.05).

	Veg. variables Parameters	Coverage	Mean height (m)	Max height	Median	Skewness	Kurtosis
7 farms	p_{bog}	0.055	0.5403	0.811	0.0137* ($t=2.76$)	0.836	0.748
	p_{farm}	0.002*	0.013*	0.019*	0.0001*	0.025*	0.017*
6 farms (40F1 excluded)	p_{bog}	0.042* ($t=2.20$)	0.223	0.21	0.032* ($t=2.39$)	0.201	0.684
	p_{farm}	0.290	0.344	0.084	0.621	0.212	0.083

Table 3. Regression results of anuran density and diversity against the bog sequence.

*** indicates the correlation is significant. Negative t values indicate the variable decreases as bogs are located farther from the reservoir.**

species factors	Spring Peeper	Green Frog	Carpenter	S. Leopard	Species richness
p _{bog}	0.803	0.643	0.035* (t=-2.24)	0.267	0.023* (t=-2.44)
p _{farm}	0.329	0.036*	0.021*	0.999	0.999

Table 4. Regression results of anuran density and diversity against vegetation variables (%coverage and average height) of bogs. The farm effect (p_{farm}) is not shown because none of the regressions exhibited significant variation among farms.

		Spring Peeper	Green Frog	Carpenter Frog	S. Leopard Frog	Total species#
% Coverage	p_{bog}	0.764	0.124	0.045* ($t=-2.15$)	0.023* ($t=-2.56$)	0.057
Ave. height	p_{bog}	0.850	0.263	0.277	0.050* ($t=-2.08$)	0.099

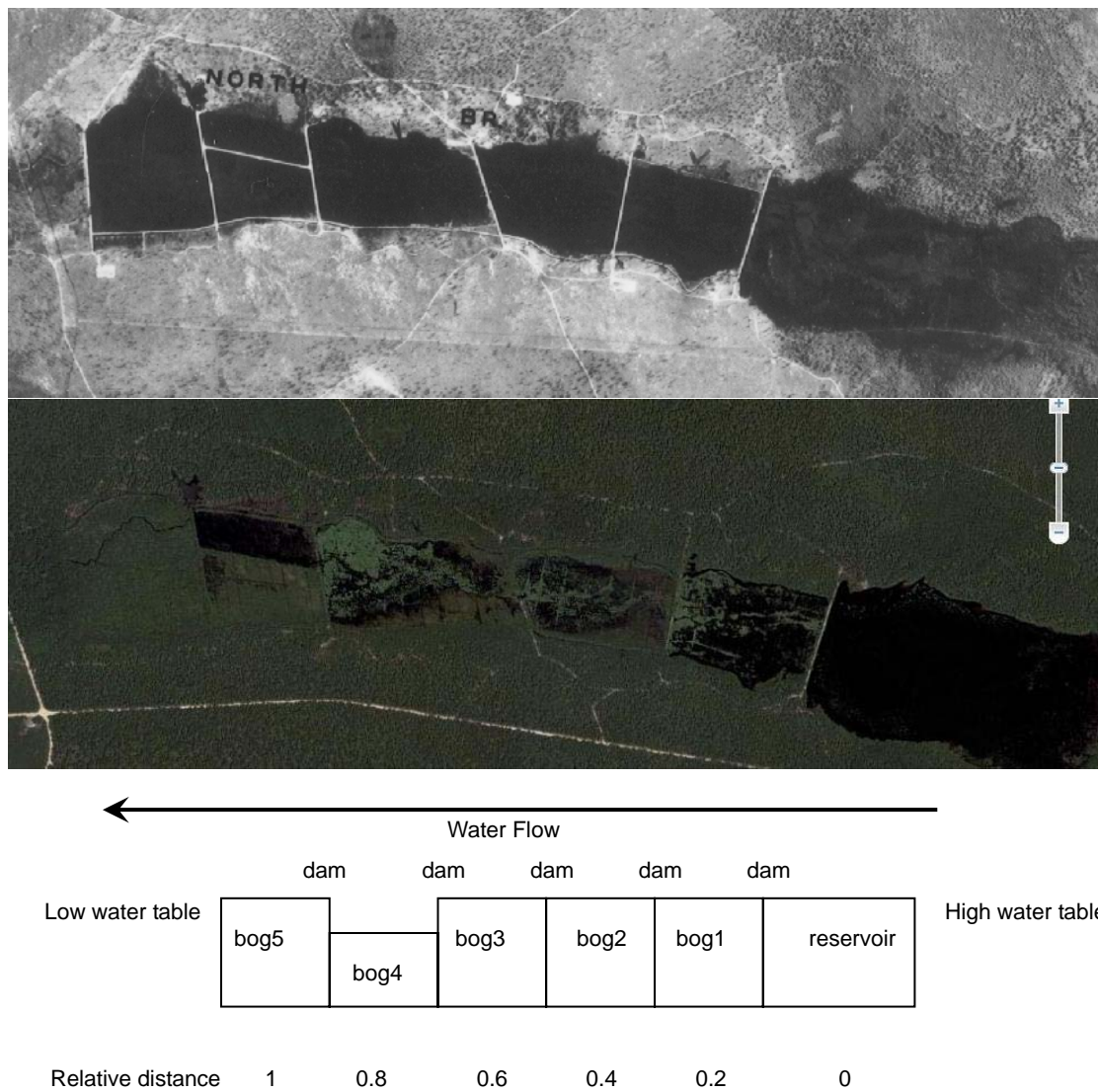


Figure 1. Air-photo of farm 30F1 in 1930s (top, when the farm was abandoned) and 2006 (bottom). Diagram shows the upstream reservoir and downstream bogs along the hydrological gradient. Dams were used to control water level when the farm was still active. The arrow indicates the direction of water flow from reservoir to the downstream bogs.

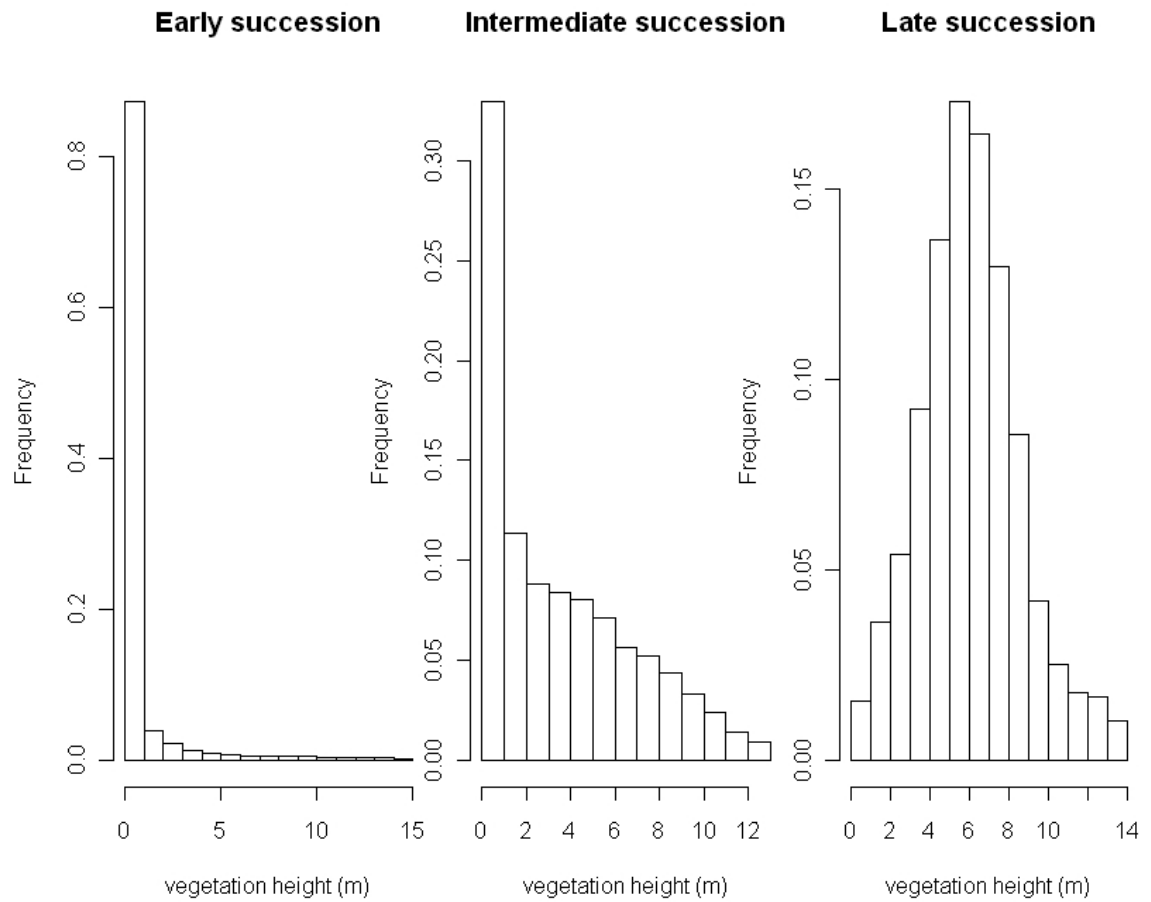


Figure 2. Histograms of the early, middle and late successional stages of the bog vegetation. Note that the y-axes have different scales.

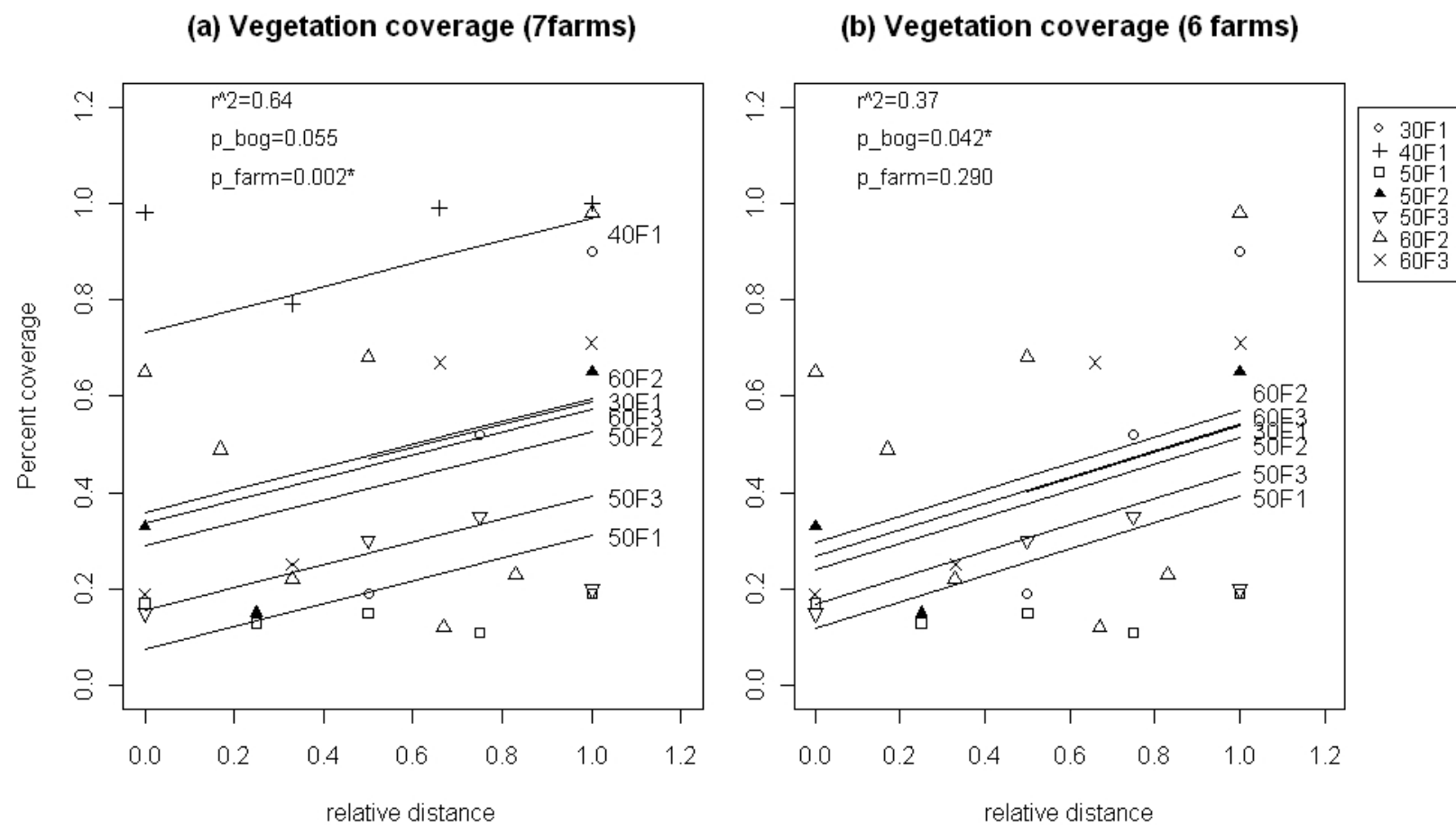


Figure 3. Vegetation coverage along the bog sequence.

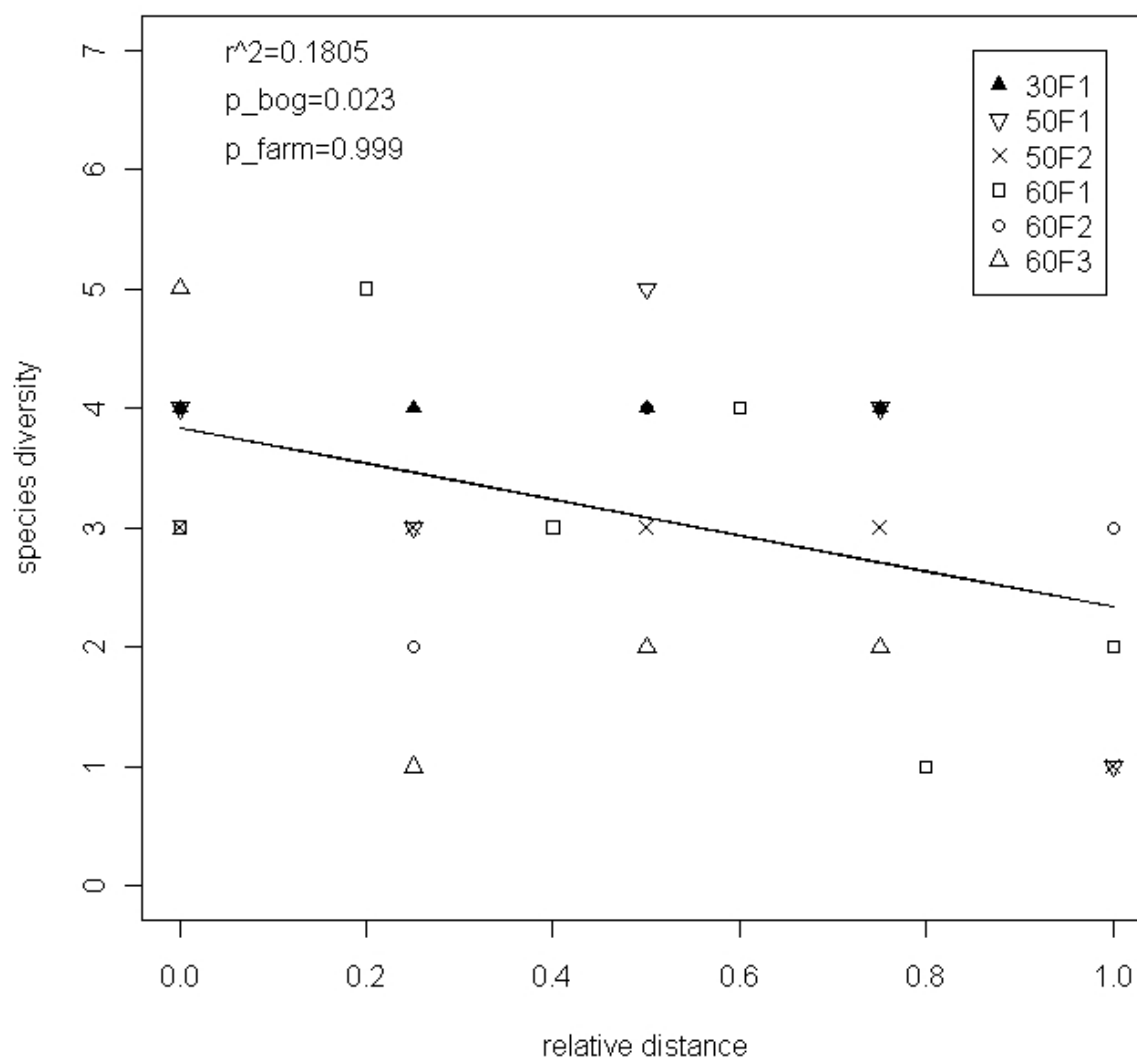
Figure4 Species richness along bog sequence

Figure 4. Correlation between species diversity and a bog's relative distance from the reservoir. Each symbol represents the species diversity in one bog, and bogs within the same farm are represented by same symbols. The line shows the regression of species diversity against relative distance, which decreases significantly as the bog is farther from the reservoir ($p_{\text{bog}}=0.023$). Species diversity does not exhibit a significant diversity variation among farms ($p_{\text{farm}}=0.449$).

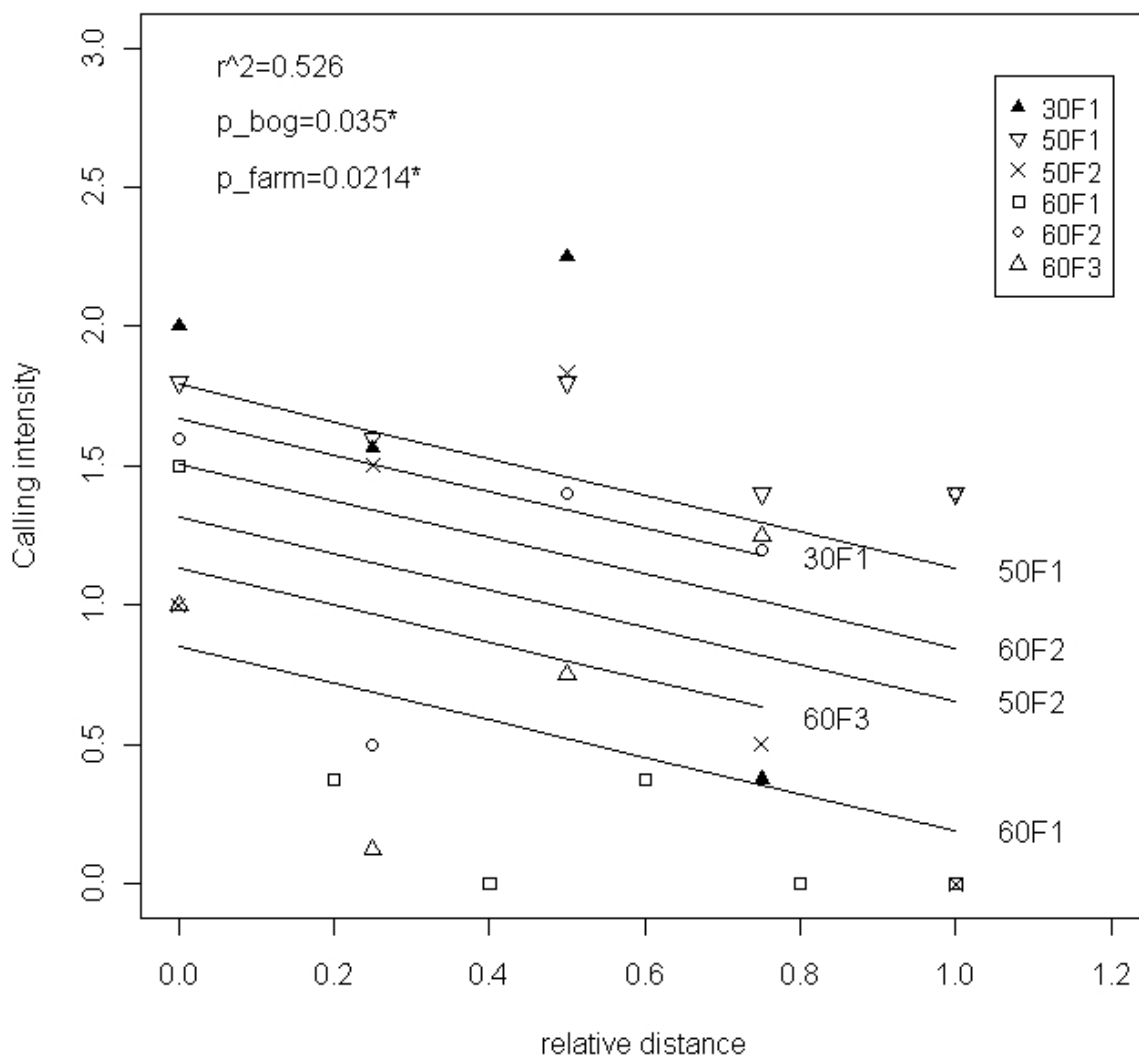
Figure5 Carpenter frog density along bog sequence

Figure 5. Correlation between carpenter frog abundance and the bog's relative distance from the reservoir. The randomization analysis shows that species density decreases as the bogs are located farther from the reservoir ($p_{\text{bog}}=0.035$). It also shows the species density varies among different farms.

CHAPTER 4

Conclusions and Implications

Cranberry farms are anthropogenic components of the Pinelands of New Jersey. The cultivation of cranberry is an important source of economic incomes for the local community of growers. Meanwhile, cranberry farms are embedded in the freshwater wetlands. Human agricultural activities unavoidably interface with the surrounding ecosystems in many ways. To address these interactions between agriculture and natural environment, this dissertation examined ecological values and impacts of cranberry farming on the natural components of the Pinelands. Although the result of this specific wetland farming system cannot be directly generalized to other agricultural systems, this study demonstrated the need to reconcile the immediate and long-term ecological functions of a farmland system.

Cranberry farms are composed of a variety of wetland habitats with different hydrological and biological characteristics. Throughout the year, various cultivation practices bring a range of abrupt modifications to these wetland habitats. These diverse habitats are utilized by anuran species with different hydrological requirements and different tolerances of human disturbance. Even the intensively cultivated cranberry beds are preferred by some anuran species that have higher tolerance to human disturbance, or can indirectly benefit from human activities. Two anuran species, *Rana clamitans* and *Bufo woodhousii fowleri*, have higher density within active farms than abandoned farms. Their abundance in active farms can be related to many human activities. Cranberry growers intensively irrigate the crops in late summer to compensate for fast water evaporation and to reduce heat damage. The irrigation creates a relatively more stable

water level in the active farms, which coincides with the more persistent calling behavior of *R. clamitans* in these habitats. Meanwhile, higher intensity of human disturbance potentially reduces the density of anuran tadpole predators. This can indirectly benefit the survival of the tadpoles of *R. clamitans* and *B. woodhousii fowleri*. Thirdly, compared with many other crop types, the cultivation of cranberry requires a lower amount of fertilizer input and more controlled pesticide application. The lower chemical contamination enables cranberry farms to be used as habitats for anurans. Although, not all anuran species benefit from human activities. *R. virgatipes*, a species that prefers reservoir habitats in both active and abandoned farms, exhibits higher density in abandoned farms. The density of another species, *R. sphenoccephala*, varies to a great degree in all habitats. *R. virgatipes* has overwinter torper, while *R. sphenoccephala* has a very early breeding period. These behaviors coincide with the intensive water management period in the fall and spring, which might have caused the lower density of these two species in the active farms.

Overall, cranberry farms provide diverse habitats that are subjected to a range of cultivation practices during all seasons. These habitats can be used by various anurans, but human activities can both bring positive or negative influences. In order to maximize the wildlife habitat function of cranberry farms, I should to maintain or increase the habitat heterogeneity within the farms. To compensate for the negative influence of human activities on some anuran species, I need to incorporate more water bodies where the cultivation practices are not applied within or adjacent to cranberry farms. Thus, cranberry farms can sustain species that benefit from human activities and species that are less tolerant to disturbance. Just as many previous studies have demonstrated in

upland farm systems, the habitat heterogeneity is the key to the thriving of farmland wildlife communities.

Agriculture's ecological impact does not decrease as the cultivation activities cease. In the abandoned cranberry farms, the modified habitat conditions play a big role in determining the succession trajectory during the initial phase of the post-agricultural stage. After 70 years of cranberry cultivation, viable seed banks of indigenous species remain in the soil. However, the accumulated soil strata during cranberry cultivation contain seed banks with a different species composition compared to the soil layer that existed before the cranberry cultivation started. Moreover, the cranberry bog's hydrological condition, represented by the post-agricultural water level, strongly affected the species composition, viability, and density of germinated plants from the soil. In addition to these abiotic legacy effects, cranberry cultivation has also biologically modified the flora in the farm habitat by introducing and increasing the population of agricultural weeds. After a farm is abandoned, colonies of weed species remain. These colonies, together with the remaining cranberry woody tissues, have created barriers to the germination of remaining seed bank within the soil.

There are a variety of restoration strategies that can be applied to restore abandoned farmlands. Flooding is a commonly applied method to restore natural wetlands because it can prohibit the germination of upland species, and consequently increase the proportion of wetland species. However, in abandoned cranberry farms, flooding treatment does not change the species composition of germinated plants or increases the viability of the seed bank. Only when viable seeds are present can flooding treatment increase the density of germinants. On the other hand, removal of weed colonies and cranberry woody tissues is

an effective method to reduce the interference from the biological remnants. It can be applied as a restoration strategy to accelerate the recolonization of plant communities from seed banks.

The legacy effect of cranberry farming is still lingering after half a century. In abandoned cranberry farms aged from 50 to 80 years, the plant and anuran communities in each bog unit still exhibit gradual changes along the bog sequence from upstream to downstream. Plant coverage and mean height increases in bogs that are located farther from the reservoir. Meanwhile, anuran diversity decreases significantly from upstream to downstream in the bog series. The densities of two anuran species, *R. virgatipes* and *R. sphenoccephala*, are negatively correlated with increased vegetation coverage and height, indicative of these species' preference for open water during breeding season. Compared to the linear pattern of these vegetation and anuran variables along the bog sequence, the among-farm differences of these variables is not strongly supported by the statistical model. The 30-year age difference of these farms does not result in obvious differences of the vegetation structure or the anuran communities. Rather, the hydrological gradient along bog units from upstream to downstream is the major determinant of the post-agricultural development of vegetation and anuran communities.

Wetland crops comprise a major agriculture type that covers a large portion of the earth. In this dissertation, I use cranberry farms to exemplify wetland agriculture's ecological functions and legacy effects. I illustrate the wetland farm's function as wildlife habitat, as well as its persisting post-abandonment effects on the ecosystem. These have not been documented in detail before. Agriculture has accompanied the human race for over 10,000 years, and will continue its services in the foreseeable human future. Studies

such as this dissertation are essential for us to enact sustainable schemes that will ensure a prosperous development of agriculture that is compatible with healthy ecosystems.

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