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Conserving biodiversity in agriculture-dominated landscapes:
Loss of natural habitat drives Lepidopteran declines at multiple spatial scales

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Conserving biodiversity in agriculture-dominated landscapes: Loss of natural habitat drives Lepidopteran declines at multiple spatial scales

by

April Amanda Melissa Feswick

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Abstract

The expansion of agriculture throughout the world has precipitated serious biodiversity losses. Countries with relatively extensive natural habitats, such as Canada, continue to intensify agricultural land uses, threatening to expand the scope of the present mass extinction. This thesis tests likely mechanisms of butterfly species decline in agricultural landscapes of varying intensities in the most biologically diverse region of Canada. I measured site variables such as the richness of plants suitable for larval development, patch area and shape index, and landscape variables such as heterogeneity and land-cover within buffers that varied in size from 100m to 1000m. Several rare species were not present in the agricultural sites, whereas a few species typically associated with disturbed habitat were present and abundant among most study sites. I found that agricultural intensification acts across landscapes to reduce butterfly species richness by reducing the proportion of natural habitat available. This effect was especially pronounced at 100m to 200m distances, suggesting a threshold effect beyond which the proportion of natural land is less critical to butterfly biodiversity. Within-site factors, such as plant species richness and habitat area were not affected by agricultural intensity, nor did they affect butterfly species richness and abundance. These results suggest that the mechanism linking butterfly species decline to agriculture, at least for butterflies in this region, is the loss of small habitat remnants.

Résumé

L'expansion et l'intensification de l'agriculture à travers le monde ont précipité une perte importante de biodiversité. Les pays, tels que le Canada, qui disposent d'un nombre relativement grand d'habitats naturels, continuent d'accroître l'exploitation de leurs terres, menaçant d'augmenter encore la portée de cette extinction de masse. Cette thèse met à l'épreuve les mécanismes probables de la perte d'espèces de papillons sur des terres à intensités agricoles variées, dans la région canadienne avec la plus grande diversité biologique. À l'intérieur de zones tampons qui varient en largeur de 100m à 1000m, j'ai mesuré des variables reliées au site, telles que la richesse des plantes qui conviennent au développement larvaire, l'aire de la zone et l'index de la forme de la zone, ainsi que des variables reliées au paysage, telles que l'hétérogénéité et les couvertures terrestres. Plusieurs espèces rares n'étaient pas présentes sur les sites agricoles étudiés, tandis que quelques espèces typiquement associées aux habitats perturbés y étaient habituellement présentes et abondantes. J'ai trouvé que l'intensification agricole agit sur l'ensemble des paysages pour y diminuer l'abondance d'espèces de papillons en y réduisant la disponibilité des habitats naturels. Cet effet a été le plus prononcé à une distance de 100m à 200m. Ceci suggère un effet de seuil, au-delà duquel la biodiversité des papillons est moins affectée par la proportion de terrain naturel. L'intensité agricole n'a eu aucun effet sur les facteurs relatifs au site, tels que la richesse d'espèces de plantes et l'aire totale d'habitats, et ceux-ci n'ont pas affecté la richesse ni l'abondance des espèces de papillons. Ces résultats suggèrent que le mécanisme liant l'agriculture à la diminution

en diversité de papillons, du moins dans cette région, est la perte de parcelle restante d'habitat naturel.

Introduction

Human activities have increased extinction rates enormously (May and Tregonning 1998). Land-use changes are likely to be responsible for the majority of future global diversity loss (Sala *et al.* 2000). The rapid expansion of industrial agriculture following the Second World War has lead to widespread conversion of complex, natural ecosystems to simplified, managed, high-output ecosystems, which represents a major threat to global biodiversity. Even in regions with relatively extensive wilderness, such as Canada, most species declines are due to agricultural activities, which also serve to limit the recovery of endangered wildlife (Kerr and Cihlar 2004; Kerr and Deguise 2004).

Agricultural land uses in Canada are concentrated in areas with high biodiversity (Kerr and Cihlar 2004). Furthermore, these agricultural land uses have undergone significant intensification, defined as 'a process of increasing the utilization or productivity of land currently under production using various chemical and technological methods' (Netting, 1993: 262). European studies, in particular, present an extensive record of species declines and extinctions that relate to this agricultural intensification process (Krebs *et al.* 1999; Robinson and Sutherland 2002; Benton *et al.* 2003; Newton 2004). The negative effects of agriculture on species richness and/or abundance have been extensively documented in mammals (Flowerdew 1997), birds (Donald *et al.* 2001; Freemark and Kirk 2001), insects (VanSwaay 1990; Fleishman *et* *al.* 1999), vascular plants (Freemark and Boutin 1995; Zechmeister *et al.* 2003), and bryophytes (Zechmeister and Moser 2001).

There has been considerable research investigating potential causes of biodiversity declines due to agriculture (e.g. Donald *et al.* 2001; Freemark and Kirk 2001; Dauber *et al.* 2005). Pesticides, fertilizers, declining habitat quality, loss of plant species, farming practices and machinery, and farm management have all been cited as partly responsible for abundance and richness declines of various organisms (Parish *et al.* 1994; Mander *et al.* 1999; Chamberlain *et al.* 2000; Newton 2004). That agricultural intensification has been a main cause of biodiversity declines in recent decades is now clear. However, the most important mechanism(s) responsible for this loss of species is not.

Many studies suggest that reductions of habitat heterogeneity in intensive, agricultural landscapes may be one mechanism for species decline (see Benton *et al.* 2003 for a review), although there are serious limitations in the empirical support of the relationship between habitat heterogeneity and species diversity (Tews *et al.* 2004). In general, these declines have been associated with increasing temporal and spatial homogeneity of landscapes, limiting habitat and resources necessary to maintain natural populations (Mander *et al.* 1999; Benton *et al.* 2003; Mayfield and Daily 2005). For example, Weibull *et al.* (2000) linked species richness losses in agricultural areas with reduced field margins and therefore reduced spatial heterogeneity. Reductions of habitat heterogeneity due to agriculture across Canada relates to species endangerment (Kerr and Cihlar 2004). In Europe, aspects of agricultural intensification (such as increased chemical applications, reduced crop rotation and larger field size) have reduced habitat heterogeneity and subsequently led to biodiversity losses (Chamberlain *et al.* 2000; Benton *et al.* 2003). The literature also suggests that simply restoring habitat heterogeneity, by planting hedgerows, reducing plowing, or similar means, could improve the conservation outlook for many species. Increasing the variety of habitats in a landscape can also help reduce habitat isolation (Ricketts 2001; Ouin and Burel 2002) by improving landscape connectivity (Ouin and Burel, 2002; Jeanneret *et al.* 2003; Weibull *et al.* 2003).

An alternative mechanism for species declines in agricultural landscapes is simple loss of habitat area, which can clearly also relate to reduced habitat heterogeneity. For example, agricultural intensification typically involves the expansion of crop area and the implementation of monocrops, resulting in relatively homogeneously planted landscapes with little non-crop area. Agricultural intensification can lead to the elimination of small non-crop habitat remnants, such as field margins, uncultivated patches, and hedgerows, which could contribute strongly to the maintenance of biodiversity (Burel 1996; Holland and Fahrig 2000; Ouin *et al.* 2000; Freemark *et al.* 2002) The specific mechanism through which non-crop area promotes biodiversity is likely increased patch connectivity via corridors to sustain metapopulations (Fry and Robson 1994; Petit and Burel 1998; Gehring and Swihart 2003) or simply by increasing habitat area (Fahrig 2001; 2003). Regardless, augmentation of non-crop habitats may increase the size of existing functional habitat patches, and consequently biodiversity, as long-established species-area relationships demonstrate (MacArthur and Wilson 1967; Blake and Karr 1987; Bruun 2000; Sawchik 2002), as well as protect sensitive species against edge effects (Parish *et al.* 1994; Millán de la Peña *et al.* 2003).

Strategies to conserve species in agricultural landscapes could draw on extensive European literature (e.g. for a review, see Benton *et al.* 2003), but those results may not apply as generally in North America. European agricultural land uses have been widespread for centuries, even millennia (Duby and Wallon 1975), leading to its distinctive ecological history and landscape structure (Krebs *et al.* 1999). The agricultural landscape is scattered with hedgerows, grasslands, and other non-crop features, especially since the implementation of new measures intended to promote farmland biodiversity (e.g. Environmental Sensitive Areas, Countryside Stewardship Scheme; United Kingdom Government 2005). Extensive agriculture in Canada is a comparatively recent phenomenon. It is heavily concentrated in the prairies and Southern Ontario and Quebec. Natural habitats remain scattered within this agricultural matrix, most of which are on private lands (for discussion, see Kerr and Cihlar 2004, Deguise and Kerr in press). By virtue of long integration, European species may be relatively well adapted to agriculture (i.e. species that remain are frequently tolerant to agriculture; Green 1979; Burel *et al.* 1998; Robinson and Sutherland 2002), whereas widespread land use conversions in North America have occurred relatively recently, so remaining species in these landscapes may lack tolerance to agricultural land uses that potentially exists among European species.

Restoring natural habitats in agricultural areas would likely reduce extinction rates, but this is unlikely to happen over very extensive areas. Because species richness frequently peaks in areas that have been largely converted to agriculture land uses (Balmford *et al.* 2001; Araújo 2003; Kerr and Cihlar 2004), conserving species successfully will often rely on successful integration of natural areas into an agricultural matrix. Achieving this goal will require the identification of specific mechanisms of species decline in recently established agricultural landscapes. Thus the first step in biological conservation requires identifying composition patterns in species assemblages in agricultural landscapes, and ascertaining the importance of local and landscape factors in predicting the composition of species assemblages.

The primary purpose of my thesis is to identify likely mechanisms of species declines in agricultural landscapes. I accomplished this by documenting Lepidopteran species richness and abundance patterns at local and landscape scales in agricultural landscapes in South-Eastern Ontario, Canada. First, I addressed whether site variables such as patch shape index (edge effect), patch area, total plant species richness, butterfly larval and adult food plant richness, and plant biomass accounted for observed changes in species diversity and abundance of butterflies. Secondly, I examined two possible mechanisms by which agricultural intensity may be influencing the butterfly community: habitat loss and habitat heterogeneity. The goal of this thesis is to isolate the relative contributions of habitat loss and habitat heterogeneity (which are not necessarily related, see Franklin *et al.* 2002) in explaining species richness patterns of butterflies between sites. I predict that differences in the amount of natural area will be primarily responsible for species declines, based on our knowledge of the importance of amount of habitat/and or area on species richness. I also predict that increasing agricultural intensity results in the loss of natural area. Furthermore, I predict that as agricultural intensity increases, resultant declines in habitat heterogeneity will reduce butterfly species richness. The specific hypotheses and predictions to be tested are as follows:

Hypothesis 1: Agriculture intensification reduces biodiversity.

Prediction 1: As agricultural intensity increases, the species richness and abundance of butterflies will decrease.

Hypothesis 2: Agricultural intensity negatively affects biodiversity by reducing habitat heterogeneity.

Prediction I: Heterogeneity will decrease as the intensity of agriculture increases.

Prediction II: An increase in heterogeneity will be positively correlated to species richness of butterflies.

Hypothesis 3: An alternate mechanism of biodiversity decline is reduced natural habitat area.

Prediction I: Non-crop habitat will decrease as the intensity of agriculture increases.

Prediction II: An increase in non-crop habitat will be positively correlated to species richness of butterflies.

Methods

Study taxon and area

Butterflies are key organisms for the monitoring of biodiversity and have become an important model taxon for expanding basic knowledge in ecology and conservation biology (Pollard and Yates 1993). They are easily surveyed and identified in the field. They are useful bioindicators; their diversity patterns are frequently consistent with those of many other species (Pearson and Carroll 1997; Kerr *et al.* 2000), and they are sensitive to local habitat characteristics and changes in habitat quality (Murphy and Ehrlich 1989; Layberry *et al.* 1998).

The study area is in south-eastern Ontario, Canada (45° 25' N, 75° 43' W; Figure 1) around the city of Ottawa. Once dominated by mixed-wood plains species (e.g. sugar maple (*Acer saccharum*), basswood (*Tilia americana*), eastern hemlock (*Tsuga canadensis*) and eastern white pine (*Pinus strobes*)), this region of Canada has been increasingly subjected to human-land uses such as urban development and intensive agriculture, leaving tracts of fragmented natural areas (which I consistently refer to as remnants, which are remaining natural areas with respect to current agricultural and/or urban uses, and not necessarily pre-European settlement conditions). Fieldwork was conducted in the Municipality of Ottawa-Carleton and the nearby counties of Stormont, Dundas, and Glengarry, located within 45km of the metropolitan area of Ottawa, Ontario, from May to August 2004. The region contains a gradient of landscapes dominated by agriculture, which include crops such as corn, soybeans, alfalfa, and hay, as well as livestock grazing.

Survey sites and local attributes

Twenty-two natural or semi-natural grassland non-linear butterfly habitat survey sites were selected (642 m^2 - 38257 m^2, mean 8363 m^2; see Appendix A for explicit location details including geographical (latitude and longitude) co-ordinates for all 22 sites). Sites were selected in consultation with local butterfly and plant systematists (Don Lafontaine, Peter Hall, Paul Catling, pers. comm.).

Potential local attributes influencing butterfly species richness and/or abundance were measured at each site, including: site area and perimeter, shape index, plant species richness (further divided into butterfly larval food plant richness and nectar (adult) food plant richness), and net primary productivity during the flight season (May-August). The shape index was calculated following Baker and Cai (1992):

$$\mathbf{P = (0.282 \times perimeter) / (area)^{1/2},}$$

where an increase in variable P is associated with increasing edge.

Survey sites were selected to be as similar as possible in natural history, topography, plant species richness, and other within-site factors. During the site selection period, reconnaissance work ensured that all sites included biologically significant habitat characteristics for butterflies, such as shaded and sunlit areas, egg deposition substrates such as shrubs and tree leaves, and both larval and nectar food sources (Layberry *et al.* 1998).

Landscape attributes

Butterfly study sites were located in either control or one of two treatment landscapes. Control landscapes were defined as having no active agriculture directly adjacent to or within 100m of a study site perimeter, and consisting of either natural meadows or old fields at least 5 years of age. The two treatment landscapes represented agricultural landscapes varying in intensity, categorized based on the dominant crop types: either forage (medium intensity) or cash (high intensity; see Boutin and Jobin 1998). There is no universal method of measuring agricultural intensification, and the concept of intensification is variously defined in the literature. However, several papers have demonstrated a link between the type of crop grown and the corresponding chemical and mechanical inputs required, suggesting that crop type can be used as a surrogate for a measure of agricultural intensity (O'Connor and Shrubb 1986; Britton 1990; Shrubb 1997; Evans 1997; Donald *et al.* 2001). For example, cash or cereal crops such as corn, wheat and soybean typically receive the highest pesticide and fertilizer treatments (Donald *et al.* 2001) and are categorized as high intensity agriculture. In total, eight butterfly study sites were located in control landscapes, six were in medium intensity sites (forage crops) and eight were in high intensity agricultural sites (cash crops).

Interviews with the farmers or land owners were held whenever possible to document agricultural land-use history, including pesticide, fertilizer and other chemical application data within the current and past growing season. For the survey season, all crops adjacent to our study sites (except control sites, which had no crops in the direct vicinity) underwent similar management regimes: mechanical tilling, fertilizer application, and for cash crops, one or two herbicide applications of RoundUp. However, past chemical applications varied depending on the schedule of crop rotation and the type of crops previously grown. Toxicological testing has not found this herbicide to be carcinogenic in humans, although its effects on insects and most other organisms are largely unknown (based on MSDS information). However, this is unlikely to affect our butterfly survey results for several reasons. First, we conducted our butterfly surveying after RoundUp was applied and the soil already tilled, so butterflies directly impacted by acute poisoning were already presumably dead. Second, RoundUp is metabolized by the plants, which soon die without leaching the active ingredients, nor is RoundUp stored in dead plant tissue likely to be readily available for butterfly consumption. The potential impacts of such herbicide treatments on butterfly species presents an avenue for further research, but was beyond the scope of this field study.

Field surveys

I used standard transect techniques when weather was most conducive to flight (e.g. no more than 40% cloud cover, light or no wind, temperatures above 13° C (see Pollard and Yates 1993) to measure butterfly species richness. All butterflies seen within the bounds of the route, and within an estimated distance of 5 m around the surveyor, were counted. Butterfly transects were conducted between 10 am – 3 pm. The location of each transect reflected the need to cover the complete range of local topographical heterogeneity (Swengel 1998). I conducted eight sampling transects in each study site between early or mid May and the end of August, with the surveys conducted no further than two weeks apart. This ensured that each species' flight season was captured and sampling effort for all species was equal among the 22 sites (Layberry *et al.* 1982). This is comparable to the sampling intensity in other butterfly surveys (e.g. Kerr *et al.* 2000; Weibull and Östman 2003). Butterfly species that could not be identified in flight were caught with a net, identified and released, or brought back to the laboratory and identified using the Butterflies of Canada Monograph (Layberry *et al.* 1998). Voucher specimens for species that were difficult to identify were collected. Butterflies were then classified as generalist or specialist species according to their larval food plant preferences, based on methods established by Hogsden and Hutchinson (2004) and Royer (2001). For example, Hogsden and Hutchinson (2004) suggest that generalist butterfly species are able to use a wider range of host plants as resources than specialists, based on statistically tested field observations. Therefore, in my thesis I labeled a butterfly as a generalist if it had several different larval plants upon which it fed, and labeled a butterfly a specialist if it had a narrow niche, that is, if it depended upon one species of larval food plant to survive. Those butterfly species appearing only once throughout any of the 22 sites were excluded from the generalist/specialist classification because a single individual may have mistakenly strayed into that habitat and it would not be possible to attribute the presence of an individual butterfly to host plant presence as reliably as repeatedly observed butterflies.

Plant surveys were conducted in each site using stratified random sampling, where sampling intensity was held constant with respect to site area. For example, the main sampling transect was 1 m wide and followed the butterfly transect line, and the rest were placed following the same orientation as the butterfly transect line, along 1 m wide transects placed at 10 meter intervals from each side of this central transect. Therefore, larger sites had more transects but each transect covers approximately the same proportion of the site. In addition to the transect survey lines, all tree and shrub species present within the site and on the perimeter were included in the plant surveys. Plant surveys were conducted three times throughout the spring/summer season, and plants were identified to species where possible using Porter (1959), Fernald (1970), Niering and Olmstead (1979), Case Jr. (1987), Preston (1989), Gleason and Cronquist (1991) and Farrar (1995). Plant species richness was further divided into adult and larval food plant lists, based on the pool of all butterflies found in this study (Tooker *et al.* 2002; Layberry *et al.* 1998).

Above-ground, herbaceous primary productivity was estimated by collecting plant biomass samples at the beginning and the end of the field season using the comparative yield method (Bonham 1989). These measurements were made to ensure that variation in primary productivity among sites did not account for observed patterns of butterfly richness, abundance or distribution (Bailey *et al.* 2004). Primary productivity was calculated by subtracting initial biomass from end of season biomass. Ten 0.5 m^2 quadrats were sampled at each site. The growing period was equal between sites, since sites were resurveyed in the same order and time frame. All samples were dried at 70°C for at least 48 hours prior to weighing. Both the area and boundaries of all 22 sites were recorded several times using a Garmin GPS (GPSmap 76S, which is accurate to 3-5m). Patch area and boundary locations were nearly identical between measurements.

Landscape Variables

Landscape-scale analyses for all 22 sites were conducted using digitized aerial photographs ranging in date from 1994-2002 and scale from (1:10 000 to 1:50 000), using the Geographical Information System ArcGIS 8 (ESRI 2002). The pixel size of these data was approximately 1 m^2 and is comparable to the highest resolution satellite data. The photographs were obtained from the City of Ottawa (http://ottawa.ca/city_services/maps/atlas/) and Natural Resources Canada (National Air Photo Library). Buffer zones of 100m, 200m, 500m and 1000m were constructed around each study site (Figure 2), and within those buffers all patches (a patch is defined as a relatively homogeneous non-linear area that differs from its surroundings) were assigned to one of the following five land use types: forest, open area (including both linear and non-linear patches of natural grassland, old fields, meadows, etc.), urban area, crop (includes orchards) and grazing area. The accuracy of this classification was assessed thoroughly by selecting 15-20 patches around every study locale and comparing the land use type within the patches to the predicted land use in the classification.

Within each buffer size, I calculated the proportional area of each land-use type and the heterogeneity of land uses. I measured heterogeneity using two methods. First, I simply counted the number of land-use types within each buffer zone. Second, I calculated the Shannon-Weiner diversity of land use types and accompanying evenness values.

The Shannon index is calculated as (Magurran 1988):

$$\mathbf{H' = -\Sigma\,(P_K)\,\ln\,(P_K)} \qquad (1)$$

where P_k = proportion of land-use type k

and evenness (Magurran 1988) is:

$$\mathbf{J = H'/\log s} \qquad (2)$$

where s = number of land-use types within each buffer zone (eg. 0-100m, 0-200m, 0-500m, 0-1000m).

Statistical Analysis:

Data were tested for spatial autocorrelation by calculating Moran's I statistics on residuals from regression models (Sawada 1999). Spatially autocorrelated residuals indicate that probability tests for regression models are unreliable and should be recalculated with fewer degrees of freedom or alternative regression models, such as conditional autoregressive models (Legendre and Legendre 1998; Lichstein *et al.* 2002). Statistical analyses were conducted using Systat v.10 for Windows (SPSS 2000). Butterfly habitat patch area and perimeter were calculated using ArcMap (ESRI 2002).

Species diversity measures (Shannon-Weiner and Evenness) were calculated for butterflies in control, forage and cash crop sites. One way ANOVAs using Tukey's multiple comparison tests were used to test the effect of agricultural intensity (control, forage and cash crop sites) on butterfly species richness, abundance, diversity and evenness, as well as test for the effects of the within-site variables and landscape variables (heterogeneity and natural area) upon species richness. If the ANOVA detected significant differences in either heterogeneity or the amount of natural area, it would provide evidence for the correct mechanism of species decline. In addition, landscape variables (heterogeneity indices, land-use type and amount) were correlated with butterfly species richness at all buffer sizes using ordinary least squares regression (Bonferroni-adjusted probabilities).

Results

A total of 3519 individuals from 43 butterfly species were observed (Appendix B). Across all eight control sites, there were a total of 35 species and 1668 individuals, while the medium intensity sites had 28 butterfly species and 815 individuals, and the high intensity sites had the lowest number of species, at 22, and 1036 individuals (See Fig 3 and 4). Butterfly species diversity was significantly higher in control than agricultural sites ($F = 11.79$, $df = 1$, $p = 0.002$), with diversity decreasing significantly as the intensity of agriculture increased ($F = 16.77$, $df = 2$, $p<0.0001$; Table 1). Two very common species, the European skipper (*Thymelicus lineola*) and the Inornate ringlet (*Coenonympha tullia*) were recorded at every site, followed by the Common sulphur (*Colias philodice*) and the Northern crescent (*Phyciodes selenis*), which were each found in 19 sites (86%).

The relative evenness of species diversity, J', within the control, medium and high intensity sites, ranged between 0.60 and 0.70 ($F = 4.02$, $df = 21$, $p = 0.035$; Table 1). This indicates that sites did not have comparable distributions of individuals among species, in part because a few species were very abundant in all, or nearly all, sites: the European skipper (*Thymelicus lineola*), Inornate ringlet (*Coenonympha tullia*) and the Common sulphur (*Colias philodice*). In contrast, nine butterfly species (20.9%) only occurred in one particular habitat patch: eight species (18.6%) were found in control sites only, and seven (16.3%) were found in agricultural sites only. When the abundance of each butterfly genus is pooled for control, medium and high intensity sites, both generalist and specialist butterfly genera are well represented in the control sites but as agricultural intensity rises, two introduced butterfly species (*Thymelicus lineola* and *Pieris rapae*) become increasingly dominant in terms of total butterfly abundance (Figure 5).

Butterfly species richness was significantly higher in control sites than agricultural sites ($F = 37.51$, $df = 1$, $p < 0.0001$) and was strongly affected by the intensity of the surrounding agriculture ($F = 27.57$, $df = 2$, $p < 0.001$; Table 1 and Figure 3). Butterfly species richness declined with increasing agricultural intensity. Butterfly abundance was also significantly different between control and agricultural sites ($F = 7.07$, $df = 1$, $p = 0.015$), with the largest difference in butterfly abundance occurring between the control and the cash crop (high intensity) sites ($F = 3.38$, $df = 2$, $p = 0.056$; see Table 1 and Figure 4).

These differences in butterfly species richness, abundance, diversity and evenness were not caused by within-site local attributes such as larval plant species richness, total plant species richness or site area, which were comparable among control, forage and cash crop sites (Table 2), and therefore not likely to be responsible for observed species richness patterns of butterflies ($P > 0.05$; see Appendix C and D). Incomplete sampling is unlikely to have caused the observed differences in species richness across the landscape: I jack-knifed my butterfly data to estimate field sampling efficiency and developed a collector's curve to assess the sufficiency of our sampling (Fig 6; Colwell 2005). This curve reaches an apparent asymptote, consistent with having comprehensively sampled the butterfly community. Within-site net primary productivity was significantly different between control and forage crop sites (Table 2), but was not correlated to butterfly species richness or abundance and therefore was excluded from further analyses.

Using the GIS landscape data, I tested whether heterogeneity and/or natural area were responsible for the reduction in butterfly species richness (Table 3). The ANOVAs revealed that as agricultural intensity increased, the amount of natural habitat within each buffer zone around a butterfly habitat patch decreased significantly (Figure 7a). When habitat heterogeneity was analyzed across the landscape, agricultural areas had higher habitat heterogeneity compared to control sites (Figure 7b), although the dominant land uses were human-based. Landscape evenness values indicate a similar trend across landscapes: as the intensity of agriculture increases, so do the evenness values, which were significant at the 100m and 1000m buffer sizes, respectively ($F = 5.35$, $df = 2$, $p = 0.014$; $F = 5.08$, $df = 2$, $p = 0.017$).

I also tested for variation in butterfly species richness as a function of both landscape heterogeneity and amount of natural area, crop area and urban area within different sized buffer zones. Initial correlations between species richness and land use at each of the buffer sizes revealed similar trends: the extent of natural area, as measured from aerial photograph and GIS data, related strongly and positively to butterfly species richness. Conversely, the extent of crop and urban areas are strongly and inversely related to butterfly species richness (Table 4).

The relationship between butterfly richness and crop extent within the 200m buffer is stronger than at any other distance ($R^2 = 0.61$, $p < 0.0001$; Figure 8). Furthermore, crop extent within any buffer distance (100m, 500m, 1000m) is not significant if included in a regression model with crop extent within a 200m buffer.

To ensure that spatial autocorrelation was not responsible for any of the relationship uncovered, Moran's I was calculated for plants and butterflies across all 22 study sites using latitude and longitude co-ordinates (Sawada 1999). Spatial autocorrelation was tested at 100 meter lag intervals up to 100 km. Residuals for final regression models of plant species richness ($I = 0.62$, $p = 0.257$) and butterfly species richness ($I = 0.16$, $p = 0.316$) were not spatially auto-correlated.

Discussion

Recent examinations of biodiversity at broad scales have proposed several mechanistic hypotheses to explain how agricultural intensification reduces biodiversity (Kerr and Cihlar 2004; Kerr and Deguise 2004). My research explicitly tested two of these mechanisms at both local and landscape scales: habitat heterogeneity and loss of natural habitat. I found that natural habitat loss at a landscape scale is the single most important mechanism of Lepidopteran biodiversity declines in agricultural landscapes.

Butterfly species richness is highly correlated with the amount of natural habitat in each of the four buffer sizes. In addition, agricultural intensity in this study was characterized by a reduction of natural habitat area and associated with significant reductions of both butterfly richness and abundance. This evidence supports my initial hypothesis that agricultural intensification causes species richness declines in Lepidoptera, as well as the hypothesis that agricultural intensity causes biodiversity declines by reducing natural habitat area. Butterfly richness decreases with increasing crop area and is most pronounced at the 200m buffer size. Between 200m and 500m buffer sizes, the crop effects on butterfly richness diminishes rapidly, suggesting a threshold effect of distance beyond which the negative consequences of agricultural intensity rapidly become less important. Although habitat loss and fragmentation are well-known, serious threats to biodiversity (Wilcox and Murphy 1985; Saunders *et al.* 1991), these data demonstrate that it is possible to increase the number of species that can coexist with intensive human land uses by maintaining patches of natural habitat (see Figure 6). Increasing agricultural intensity reduces butterfly species richness through erosion of natural habitat remnants, suggesting that conserving biodiversity in even highly intensive agricultural landscapes is possible if some natural habitat remnants can be maintained.

This work on mechanisms of species loss in agricultural landscapes complements other studies showing the importance of natural habitat remnants within the landscape matrix (Meyer *et al.* 1998; Bruun 2000; Fahrig 2001). For example, Ricketts *et al.* (2001) showed that moth species richness and abundance was significantly higher in agricultural sites that were closer to forest than those further away from non-crop habitat. Since butterflies are mobile species, the increase in non-crop habitat may increase habitat connectivity, offsetting the impacts of agricultural land uses, such as row crops (e.g. corn), that are inhospitable to butterflies and that are barriers to dispersal (Ricketts 2001; Schtickzelle and Baguette 2003). In a European agricultural landscape, Dover (1990) demonstrated that 98% of all butterflies he observed did not stray further than 5m from the non-crop habitat they occupied. Similarly, Fry and Robson (1994) demonstrated that butterfly populations avoid crop area and use the corridor system of hedgerows for movement around the farmland. Although habitat fragmentation contributes to species loss, this research indicates that habitat loss *per se* matters more and may reach a threshold beyond which species richness collapses very rapidly (see Fahrig 2002; Sawchik *et al.* 2002).

While heterogeneity may be important at broader scales for maintaining high biodiversity (Kerr and Cihlar 2004; Kerr and Deguise 2004), at the landscape scale this becomes less important. The hypothesis that agricultural intensification causes biodiversity declines by reducing habitat heterogeneity is therefore falsified. Agricultural sites tended to be more heterogeneous, but habitat heterogeneity was unrelated to butterfly species richness in all buffer sizes ($p>0.22$). Natural habitat extent within a 200m buffer explained 69% of the variation in butterfly species richness. When landscape heterogeneity was incorporated into the model, only an additional 5% was explained, demonstrating its limited influence in shaping butterfly richness patterns. However, the sample size is small for this type of analysis and these results should be considered provisional. Butterflies are organisms that require different land types in order to meet the physical requirement posed by each stage in their life cycle (Jeanneret *et al.* 2003), a possible reason why heterogeneity is often correlated with butterfly species richness. However, the quality of habitat types must also be considered (Dauber *et al.* 2005), especially if the organisms must use specific habitat types to disperse (Holland and Fahrig 2000; Ricketts 2001). Most land use types in our study were unsuitable for most butterfly species, except for a few "weedy" species, like Cabbage Whites (*Pieris rapae*). These species are widespread and characteristic of disturbed habitats. Heterogeneous landscapes must include a portion of useable habitat, such as non-crop or lightly grazed and managed pastures, in order to benefit organisms such as butterflies (Bender and Fahrig 2005; Mayfield and Daily 2005).

Intensive agriculture was unfavourable to the butterfly fauna, as indicated by the low species diversity and the high abundance of introduced species in the community, which is consistent with community structure trends expected in disturbed ecosystems (Odum 1985). This is a direct result of a disproportionate loss of rare species from butterfly habitats in agriculturally intense landscapes. Control sites contain more specialist species than do agricultural sites (Figure 5). The proportion of introduced species also increases with agricultural intensity, probably because of an increase in the abundance of their food plants, which are grasses, mustards, alfalfa, clover and vetch - mostly planted crops.

Butterfly evenness decreases as agricultural intensity increases. Increasingly disturbed landscapes have been characterized by Hogsgen and Hutchinson (2004) as having decreased butterfly species richness while exhibiting an increase in the dominance of certain butterfly species. Fleishman *et al.* (1999) also observed lower evenness of butterfly communities associated with an increased abundance of dominant species in agricultural riparian habitats compared with relatively undisturbed non-agricultural riparian habitats. Feber *et al.* (1997) document an association between pest butterfly species abundance and agricultural habitats, as opposed to a more evenly distributed abundance of several butterfly types in less intense, organic farming systems. There are other potential negative effects of agricultural intensification besides the obvious biodiversity loss. Lower species diversity and/or changes in the natural community composition (such as the introduction of exotic species) as witnessed in these intense agricultural landscapes can impair processes such as pollination and perhaps even ecosystem functioning itself (Vitousek 1990). Future research should be geared towards ascertaining the threshold levels of these services required to sustain agricultural and ecosystem productivity.

Site variables, such as the variety of larval or adult food plants, did not relate to butterfly species richness. However, the study was designed so that sites surveyed did not differ significantly with regard to plant species richness, which clearly can affect butterfly presence (Layberry *et al.* 1998; Fred and Brommer 2003), nor were there consistent, qualitative differences in habitat patches in different milieus. Instead, spatial variation in butterfly species richness can be predicted with factors best measured across landscapes (amount of crop and natural habitat within 200m), and not within sites. Furthermore, it appears that the intensity of agriculture, from the perspective of butterflies, depends on how completely agricultural land uses remove remnant habitat patches across the landscape, rather than by its degree of mechanization, pesticide use, fertilizer application, and so on.

Study site area was not correlated with butterfly species diversity, contrary to expectations from widely observed species-area relationships (MacArthur and Wilson 1967; Sawchik 2002). Individual patch area may relate poorly to the resource needs of butterfly populations, due to their numerous habitat type requirements and mobility (Delettre *et al.* 1998). Landscape-scale habitat availability is more significant although the diversity of butterflies within a site appears to be affected little by the potentially suitable habitats beyond a threshold of approximately 200m. No evidence of edge effects was detected in this study: the amount of patch edge was unrelated to the richness of either plants or butterflies. Others have found edge or shape index to be a useful measure of habitat quality or suitability (Temple 1986; Burke and Nol 1998) affecting the diversity of various organisms (Baz and Garcia-Boyero 1995; Östman *et al.* 2001). Edge effects in non-forest habitats, even when the surrounding area is predominantly intensive agriculture, had no discernable impact on butterfly diversity, further suggesting that the mechanism for species decline in these landscapes is loss of natural habitat area. The lack of evidence for edge effects on butterfly communities in these open habitats suggests that habitat fragmentation matters less than habitat area.

There are at least two areas where additional data, had it been practical to collect, could have improved our results. First, adding more study sites would have been helpful by improving statistical power and possibly by enabling analyses of landscape connectivity and fragmentation, which could have yielded important information regarding optimal natural area configuration for conservation. Secondly, a very high resolution and thematically detailed land cover classification for this area might have enabled the detection of a significant effect of habitat heterogeneity, if one exists.

Genetically modified crops are thought to have potential negative effects above and beyond the previously examined plethora of variables affecting biodiversity (Groot and Dicke 2002; Hails 2002). In particular, crops such as corn are engineered to contain *Bacillus thuringiensis* (Bt) delta-endotoxins, which have negative impacts on species such as the monarch butterfly (*Danaus plexippus*; Hansen Jesse and Obrycki

2000). The effects of these crops in Canadian agricultural landscapes should be examined further to assess the overall risk to biodiversity.

Conclusion

These results suggest that the mechanism linking butterfly species decline to agriculture is the loss of small habitat remnants. Within-site factors, such as plant species richness and habitat area did not vary with agricultural intensity, nor did they affect butterfly species richness or abundance in this study. Although previous work suggests that agriculture reduces biodiversity through a decline in habitat heterogeneity (Ouin and Burel 2002; Benton *et al.* 2003), no aspect of habitat heterogeneity is related to butterfly species richness after accounting for crop area. In Canada, the majority of endangered species are found in agricultural landscapes (Kerr and Cihlar 2004). Thus, agricultural practices, even when very intensive, should be modified to improve the retention of habitat remnants, a strategy that could greatly improve the conservation outlook for biodiversity in Canada and elsewhere.

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Table 1: Means ± standard errors presented for butterfly richness, abundance, diversity and evenness across each site category. The P values derived from one way ANOVAs demonstrate whether there are significant differences in butterfly data between the three sites. Diversity was measured as Shannon-Weiner (H) and Evenness (J). DF = 2 in all cases.

	Treatment				
Butterfly:	**control**	**forage**	**cash**	**Anova P**	**F**
Richness	19.75 ± 1.13	13.34 ± 1.31	9.38 ± 0.71	<0.001	27.55
Abundance	208.5 ± 29.84	135.83 ± 15.52	129.50 ± 21.79	0.056 [a]	3.37
Diversity	2.0 ± 0.09	1.8 ± 0.10	1.4 ± 0.07	<0.001	16.76
Evenness	0.67 ± 0.03	0.70 ± 0.04	0.60 ± 0.02	0.035	4.02

[a] Marginally non-significant between the three treatment groups (P = 0.056); significant when compared between control versus agricultural sites (P = 0.042)

Table 2: Mean ± S.E. values and P values derived from one way ANOVAs are presented for within-site factors in the control, forage (medium intensity) and cash crop (high intensity) sites. SR= species richness. DF = 2 in all cases.

	Treatment				
	control	**forage**	**cash**	**Anova P**	**F**
Nectar SR	32.13 ± 2.83	41.17 ± 2.71	35.5 ± 3.52	0.478	0.76
Larval SR	32.88 ± 2.55	35.67 ± 1.80	29.13 ± 2.62	0.210	1.69
Total Plant SR	58.75 ± 3.59	59 ± 3.08	48.25 ± 5.18	0.142	2.16
Plant Biomass	34.07± 8.66	60.36 ± 4.83	37.25 ± 5.66	0.034	3.83
Site Area (m^2)	6511 ± 3148	11520 ± 5424	7849 ± 2648	0.636	0.46
Site Perimeter (m^2)	328.7 ± 65.8	491.3 ± 88.6	381.8 ± 47.9	0.261	1.44
Shape Index	1.53 ± 0.10	1.46 ± 0.09	1.36 ± 0.06	0.344	1.13

Table 3: Mean ± S.E., P and F values for landscape factors at the four buffer sizes: 100m, 200m, 500m and 1000m and across treatment groups. Landscape heterogeneity values are given as 10^1. DF = 2 in all cases.

		Treatment			
	control	**forage**	**cash**	**Anova P**	**F**
Heterogeneity 100m	3.86 ± 0.54	5.89 ± 0.50	5.65 ± 0.50	0.023	4.58
Heterogeneity 200m	4.10 ± 0.79	6.34 ± 0.53	6.07 ± 0.38	0.032	4.12
Heterogeneity 500m	4.12 ± 0.87	6.95 ± 0.42	6.74 ± 0.35	0.007	6.46
Heterogeneity 1000m	4.57 ± 0.81	6.67 ± 0.41	6.98 ± 0.17	0.010	5.88
Natural Area 100m	88.77 ± 6.75	28.08 ± 11.08	20.68 ± 5.63	<0.0001	25.67
Natural Area 200m	87.78 ± 8.44	32.99 ± 9.29	20.61 ± 3.81	<0.0001	25.72
Natural Area 500m	90.56 ± 6.18	44.82 ± 6.64	25.67 ± 3.98	<0.0001	38.47
Natural Area 1000m	90.40 ± 4.38	58.07 ± 5.35	31.42 ± 4.01	<0.0001	47.53

Table 4: Pearson correlations between butterfly species richness and landscape variables (natural area, crop (which includes grazing area) and urban area) within the 100m, 200m, 500m and 1000m buffer zones around the 22 study sites.

Buffer Size	Natural	Crop	Urban
1000m	**0.836**	**N/S**	**-0.703**
500m	**0.785**	**-0.659**[a]	**-0.737**
200m	**0.713**	**-0.742**	**N/S**
100m	**0.714**	**-0.739**	**N/S**

[a] Marginally non-significant: $p=0.065$

Figure 1: Map of the Ottawa region of southern Ontario, Canada, showing the location of the control (hexagons) and agriculture (triangles) study sites. The black areas represent urban area, the lighter grey represents natural habitat, and the darker grey areas represent agricultural land use.

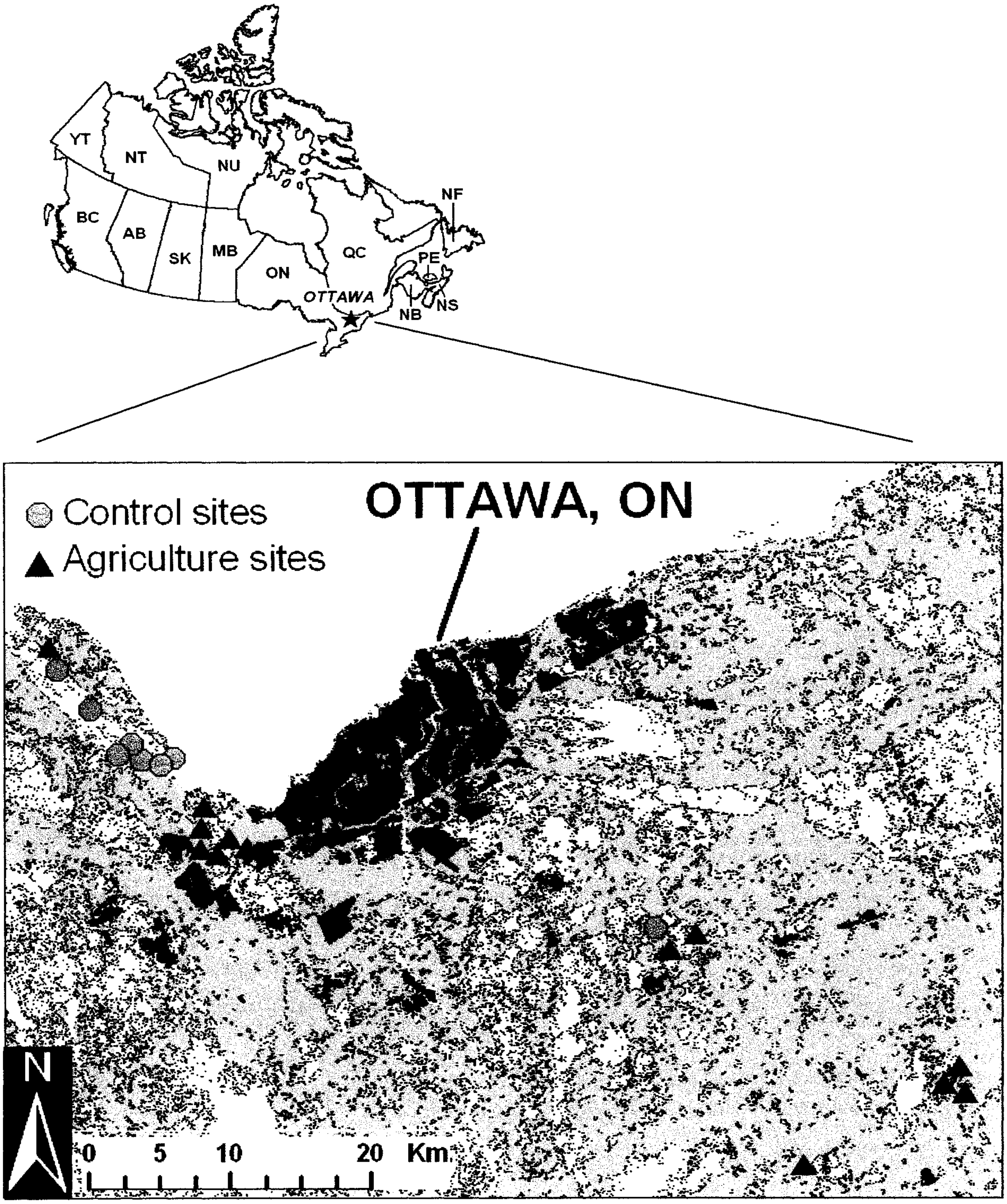

YT
NT
NU
NF
BC
AB
SK
MB
ON
QC
PE
NS
NB
OTTAWA
Control sites
Agriculture sites
OTTAWA, ON
N
0
5
10
20
Km

Figure 2: Map of control site no.8, showing each buffer zone.

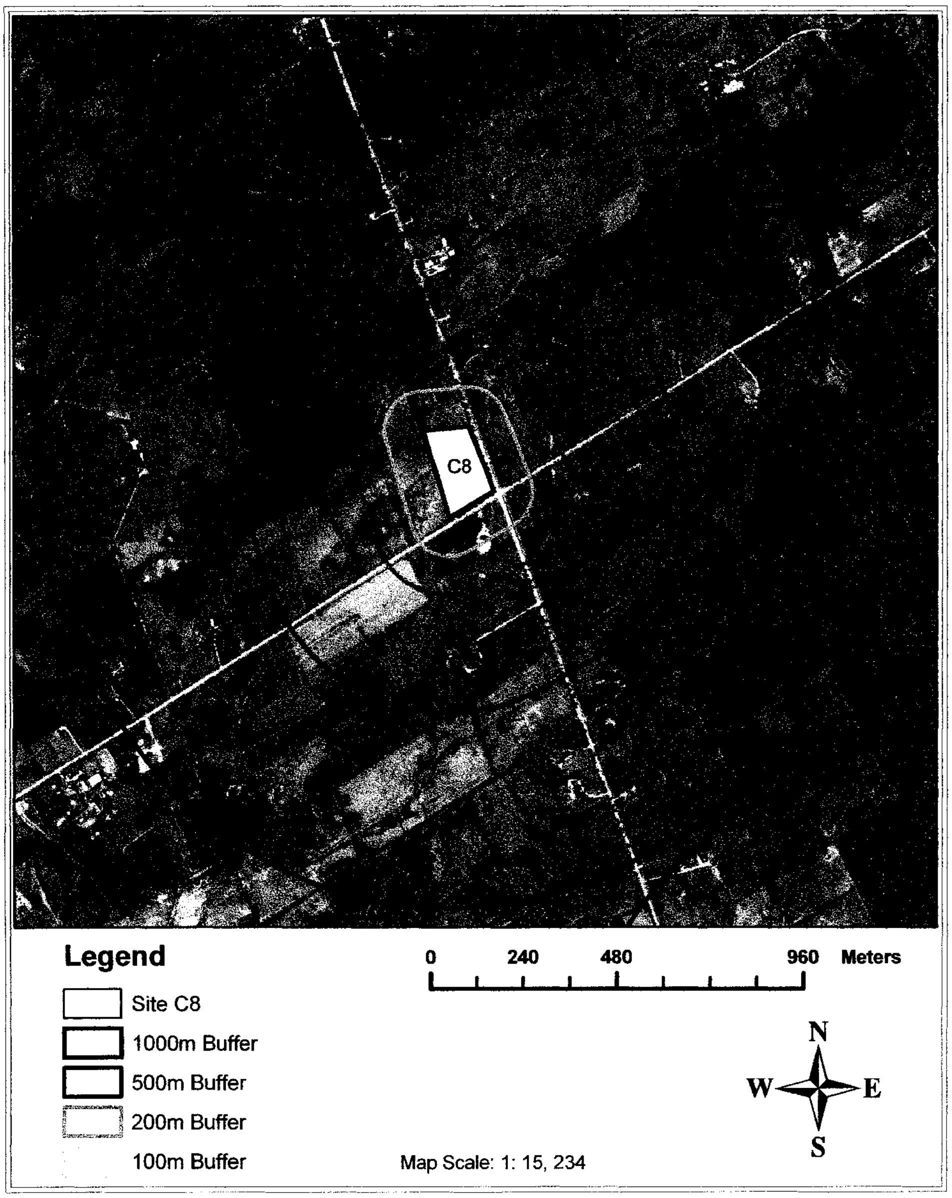

C8
Legend
Site C8
1000m Buffer
500m Buffer
200m Buffer
100m Buffer
0
240
480
960
Meters
Map Scale: 1: 15, 234
N
W
E
S

Figure 3: Butterfly species richness grouped according to site: control, medium (forage) and high (cash crop). As agriculture becomes more intense, butterfly species richness decreases rapidly. Mean ± standard error shown.

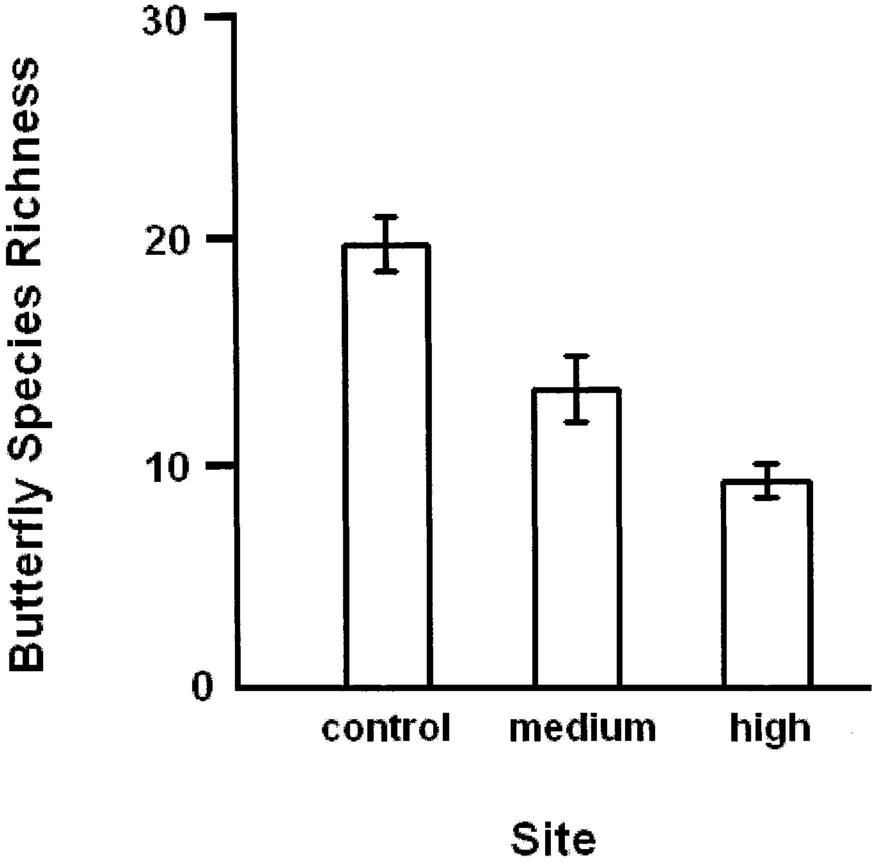

30
20
10
0
Butterfly Species Richness
control
medium
high
Site

Figure 4: Butterfly abundance grouped according to site: control, medium (forage) and high (cash crop). As agriculture becomes more intense, butterfly abundance decreases, but the only significant differences are between control sites and high intensity sites (See Table 1). Mean ± standard error shown.

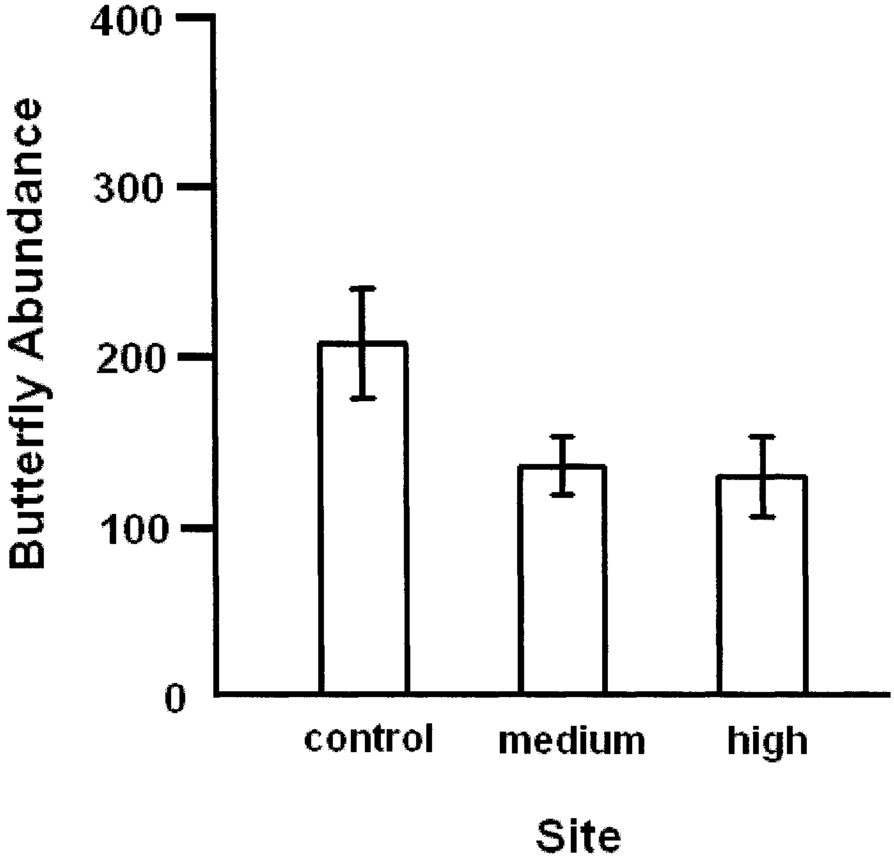

400
300
200
100
0
Butterfly Abundance
control
medium
high
Site

Figure 5: Community composition (from pooled abundance data) of control, medium and high intensity sites.

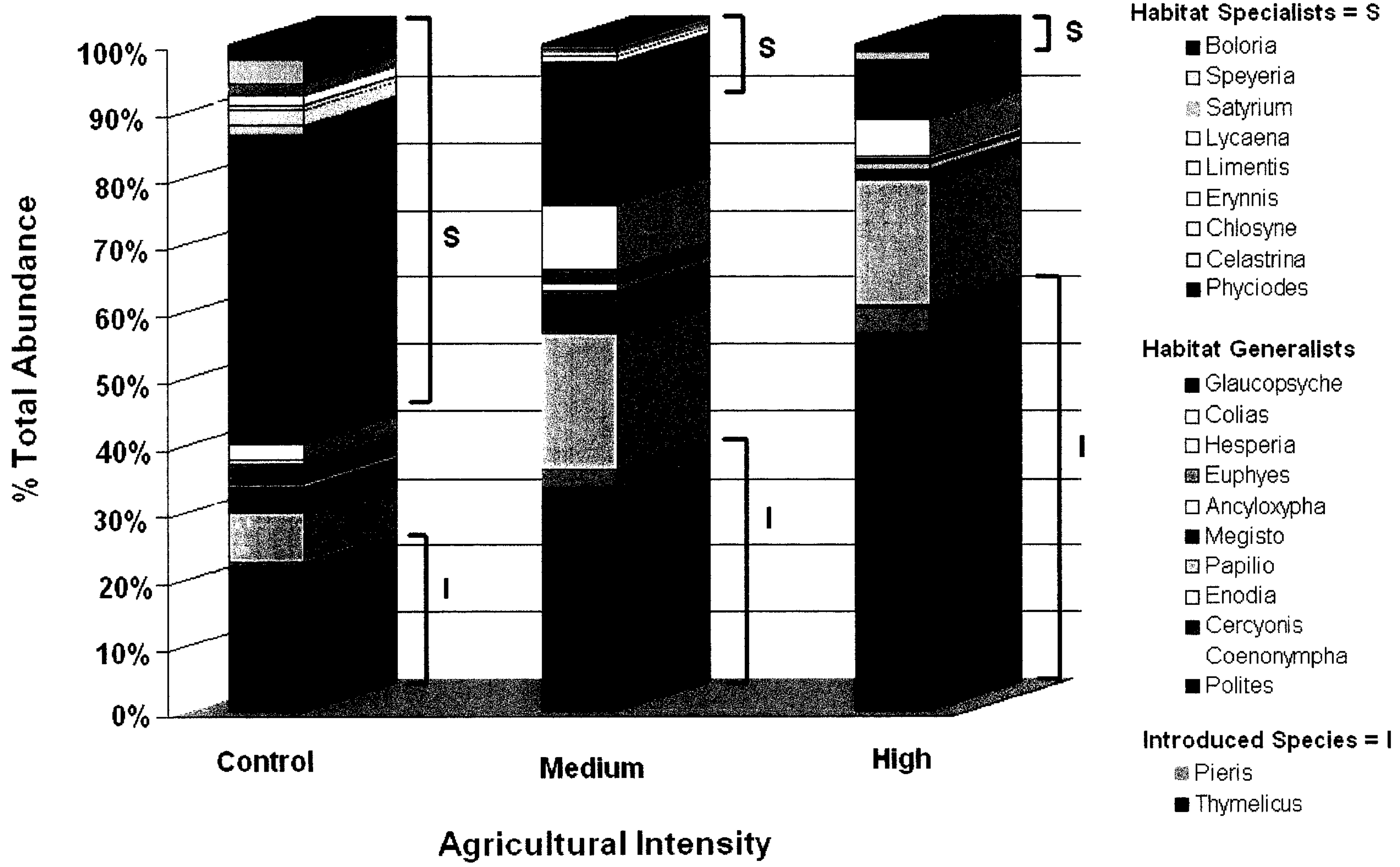
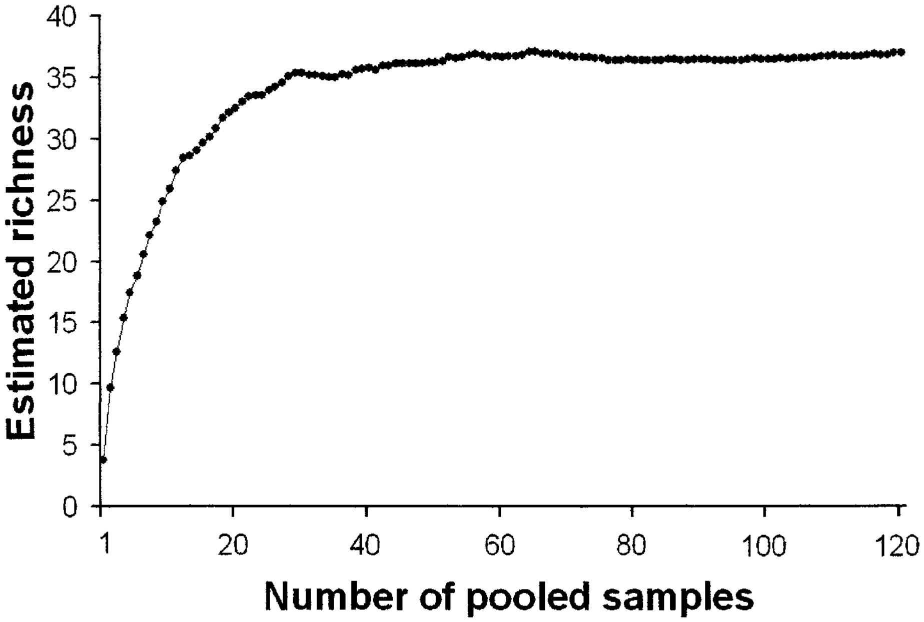

% Total Abundance
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
S
I
S
I
S
I
Control
Medium
High
Agricultural Intensity
Habitat Specialists = S
■ Boloria
☐ Speyeria
▨ Satyrium
☐ Lycaena
☐ Limentis
☐ Erynnis
☐ Chlosyne
☐ Celastrina
■ Phyciodes
Habitat Generalists
■ Glaucopsyche
☐ Colias
☐ Hesperia
▨ Euphyes
☐ Ancyloxypha
■ Megisto
▨ Papilio
☐ Enodia
■ Cercyonis
Coenonympha
■ Polites
Introduced Species = I
▨ Pieris
■ Thymelicus

Figure 6: Jack-knife estimation of butterfly species richness across all twenty-two study sites in Ottawa, Ontario. This curve suggests that few or no species were missed during butterfly surveys.

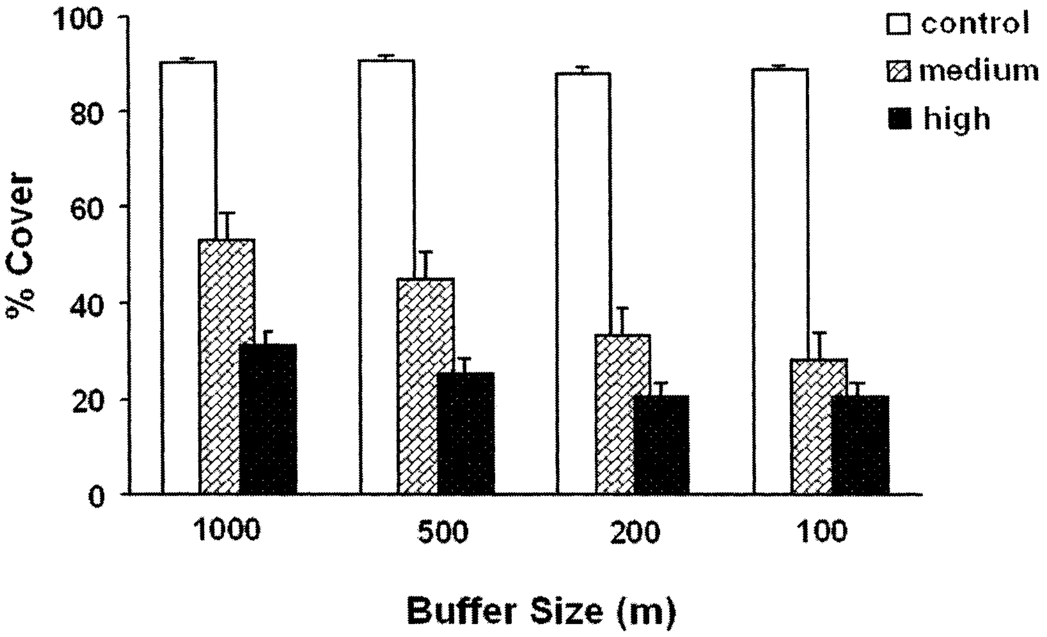


Estimated richness
40
35
30
25
20
15
10
5
0
1
20
40
60
80
100
120
Number of pooled samples

Figure 7: (a) Total amount of natural area (given as a percentage) + S.E. present in the four buffer sizes for control, medium and high intensity sites.

(b) Heterogeneity values + S.E. for control, medium and high intensity sites in the 4 different buffer sizes.

7a)


100
80
60
40
20
0
% Cover
1000
500
200
100
Buffer Size (m)
control
medium
high

7b)

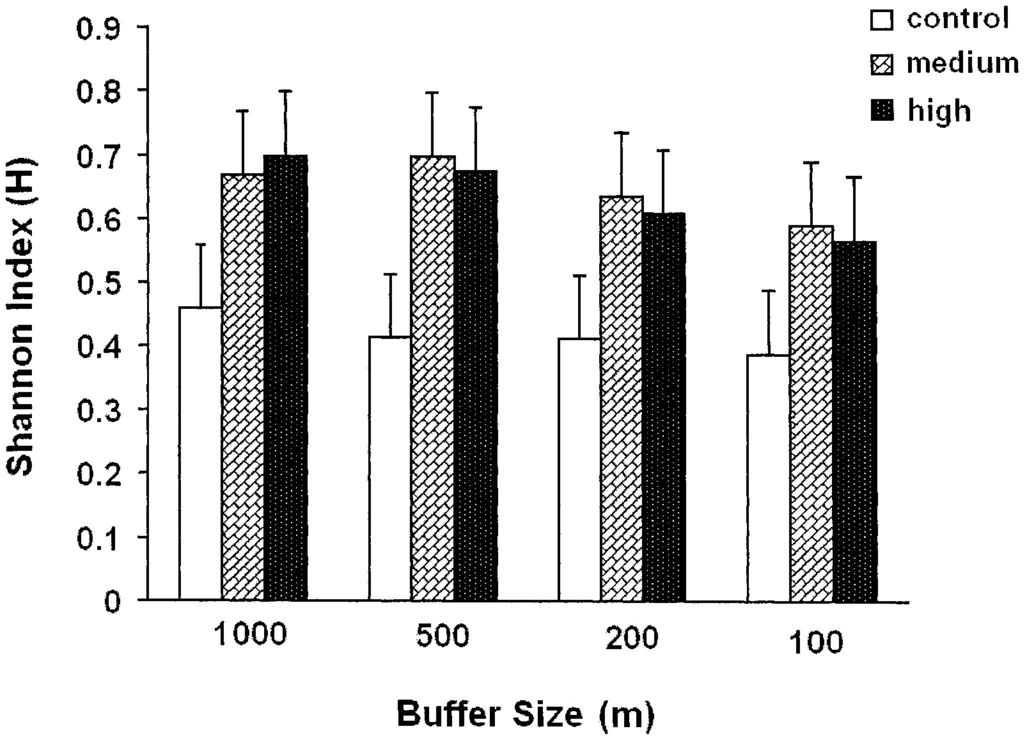
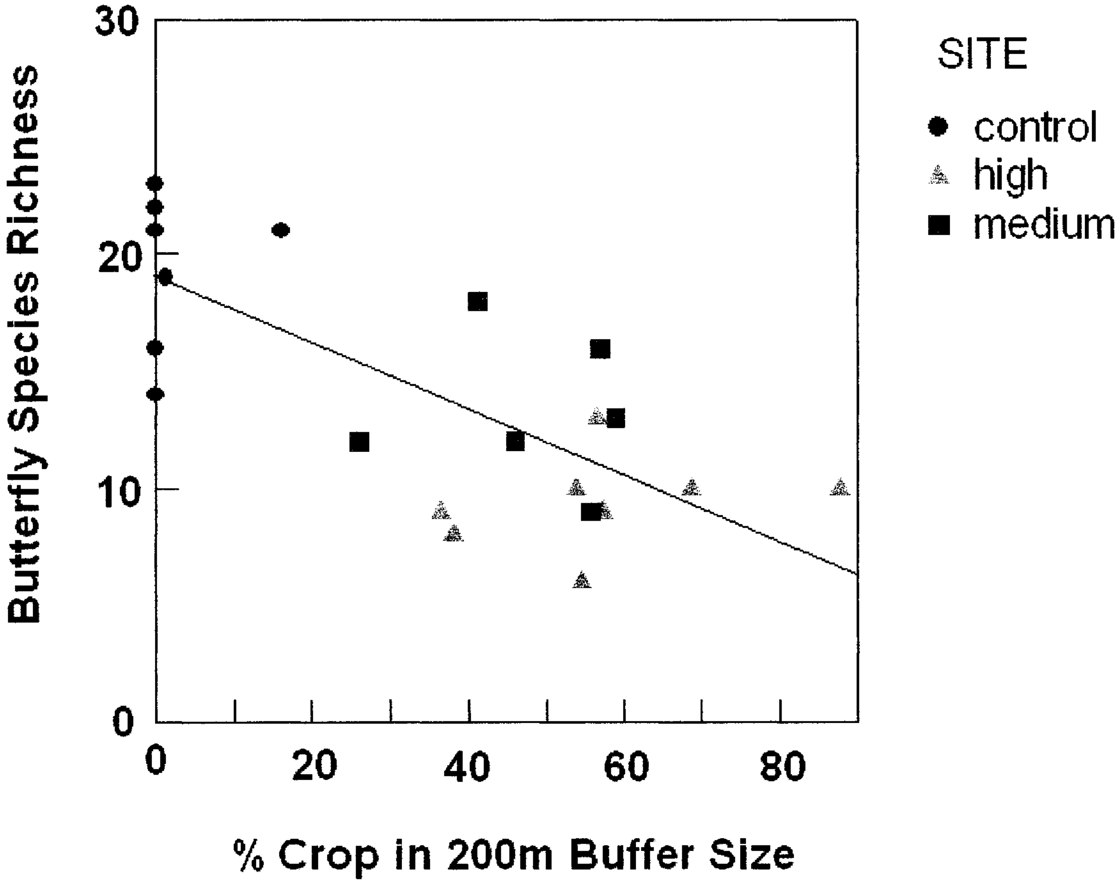

0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Shannon Index (H)
1000
500
200
100
Buffer Size (m)
control
medium
high

Figure 8: The amount of crop present within 200m of a butterfly habitat patch statistically accounts for 60.9% of the variance in butterfly species richness.


30
20
10
0
Butterfly Species Richness
0
20
40
60
80
% Crop in 200m Buffer Size
SITE
● control
▲ high
■ medium

Appendix A: Specific location of all 22 butterfly survey sites in the Ottawa area. Latitudinal coordinates are given in decimal degrees, as measured by Garmin GPS 76S MAP. These measurements are correct to within ~5 metres.

Site	Latitude	Longitude	Descriptive location
C1	45.3943	-75.9422	On Kerwin Rd., off of nature path (near school bus sign, on the same side of the road). Last site on path, beside water
C2	45.3926	-75.9450	as above; second last site
C3	45.3929	-75.9481	as above; third last site
C4	45.3934	-75.9496	as above; second site
C5	45.3938	-75.9528	as above; first site along path
C6	45.4064	-75.9563	Across the road from 655 Kerwin Rd.
C7	45.4605	-75.9994	Beside treelot on property3163 Torwood Rd.
C8	45.2625	-75.4600	On corner of 9th line Rd. and Pana Rd.
M1	45.4613	-76.0039	Opposite driveway on property 3163 Torwood Rd. and abutting a large agricultural field
M2	45.2474	-75.4451	8730 Victoria St. on Erin Holtz property
M3	45.1656	-75.2090	Corner site on Finch-Concession 7-8
M4	45.1627	-75.2151	on Finch-Winchester Boundary Road; borders Finch-Concession 7-8
M5	45.1640	-75.2159	on Finch-Winchester Boundary Road; abutting ATV path
M6	45.0825	-75.3098	Beside parking lot at 12535 Cty. Rd. 43, Winchester
H1	45.3234	-75.8839	On Corkstown Rd., beside huge field on corner
H2	45.3257	-75.8823	at the end of the lane off of Corkstown Rd.,
H3	45.3378	-75.8937	Behind houses on Bayfield Ave.
H4	45.3318	-75.8919	Off Herzberg Rd. on the apple orchard property
H5	45.3266	-75.8872	Past the first corner of Corkstown Rd. beside nature trail and field.
H6	45.3160	-75.8803	on the corner of Timm Rd. and March Rd.
H7	45.3263	-75.8735	Corner site abutting trees at the bottom of the hill on Corkstown Rd.
H8	45.2446	-75.4227	Past bridge on Murphy's Road, abutting stream (Howat's house)

Appendix B: List of all 43 butterfly species and their total abundance (grouped by treatment) caught in the Ottawa region.

Scientific Name	Common Name	control	forage	cash
Celastrina ladon	Spring Azure	14	0	1
Celastrina neglecta neglecta	Summer Azure	8	1	1
Cercyonis pegala	Common Wood-Nymph	37	46	15
Chlosyne harrisii	Harris's Checkerspot	1	0	0
Chlosyne nycteis	Silvery Checkerspot	39	0	0
Colias philodice	Common Sulphur	39	80	57
Glaucopsyche lygdamus	Silvery Blue	36	111	69
Enodia anthedon	Northern Pearly-Eye	4	1	3
Erynnis juvenalis	Juvenal's Duskywing	9	0	0
Erynnis lucilius	Columbine Duskywing	1	0	0
Everes comyntas	Eastern Tailed Blue	0	0	1
Papilio glaucus	Eastern Tiger Swallowtail	7	2	1
Papilio polyxenes	Black Swallowtail	0	2	7
Pieris napi	Veined (Mustard) White	1	4	2
Pieris rapae	Cabbage White	5	16	36
Coenonympha tullia	Inornate Ringlet	122	159	194
Danaus plexippus	Monarch	0	1	0
Limentis archippus	Viceroy	15	2	0
Limenitis arthemis	White Admiral	14	4	3
Lycaena hyllus	Bronze Copper	0	4	0
Lycaena phlaeas	American Copper	0	1	0
Megisto cymela	Little Wood-Satyr	16	2	6
Phyciodes selenis	Northern Crescent	407	50	8
Phyciodes tharos	Pearl Crescent	330	13	8
Polygonia progne	Grey Comma	1	0	0
Satyrium acadicum	Acadian Hairstreak	3	4	0
Satyrium lyparops	Striped Haristreak	1	0	0
Satyrium titus	Coral Hairstreak	19	0	1
Boloria bellona	Meadow Fritillary	27	4	15
Boloria selene	Silver-Bordered Fritillary	12	0	0
Speyeria atlantis	Atlantis Fritillary	10	0	0
Speyeria aphrodite	Aphrodite Fritillary	22	1	0
Speyeria cybele	Great Spangled Fritillary	31	2	11
Ancyloxypha numitor	Least Skipper	6	9	2
Carterocephalus palaemon	Arctic Skipper	1	0	1
Euphyes vestris	Dun Skipper	48	16	3
Hesperia sassacus	Indian Skipper	10	0	0
Poanes hobomok	Hobomok Skipper	1	0	1
Polites mystic	Longdash Skipper	2	1	1
Polites origenes	Crossline Skipper	1	1	0
Polites peckius	Peck's Skipper	0	0	3
Polites themistocles	Tawny-Edged Skipper	0	1	0
Thymelicus lineola	European Skipper	368	277	586
Total abundance/treatment		**1668**	**815**	**1036**

Appendix C: Butterfly larval food plants based on the pool of all butterflies found in this study.

Scientific Name	Common Name	control	forage	cash
Achillea millefolium	Yarrow	✓	✓	✓
Agrostis gigantea	Red Top Grass	✓	✓	✓
Agrostis stolonifera	Creeping Bentgrass	✓	✓	
Asclepias incarnata	Swamp Milkweed		✓	
Asclepias syriaca	Common Milkweed	✓	✓	✓
Aster spp.	Wild Aster	✓	✓	✓
Bromus inermis	Smooth Brome Grass	✓	✓	✓
Capsella bursa-pastoris	Shepherd's Purse			✓
Carex granularis	Meadow Sedge	✓	✓	✓
Carex lupulina	Common Hop Sedge		✓	✓
Carex scoparia	Lance Fruited Oval Sedge	✓	✓	✓
Carex vulpinoidea	Brown Fox Sedge	✓	✓	✓
Carex spp.	Sedge		✓	
Chrysanthemum leucanthemum	Oxeye Daisy	✓	✓	✓
Cirsium spp.	Thistle	✓	✓	✓
Dathonia spicata	Poverty Oat Grass	✓		✓
Daucus carota	Queen Anne's Lace	✓	✓	✓
Elymus villosus	Silky Wild Rye			✓
Elytrigia (agropyron) repens	Quickgrass	✓	✓	✓
Erigeron annuus	Daisy Fleabane	✓	✓	✓
Erigeron philadelphicus	Philadelphia Fleabane	✓	✓	✓
Fragaria virginiana	Virginia Strawberry	✓	✓	✓
Glyceria canadensis	Rattlesnake Grass	✓	✓	
Glyceria striata	Fowl Mannagrass	✓		
Lepidium virginicum	Common Peppergrass	✓		✓
Linaria vulgaris	Butter-and-Eggs	✓	✓	✓
Lotus corniculatus	Birdsfoot Trefoil	✓	✓	✓
Medicago lupulina	Alfalfa (yellow)	✓	✓	
Medicago sativa	Alfalfa (purple)	✓	✓	✓
Melilotus albus	White Sweet Clover	✓	✓	✓
Melilotus officinalis	Yellow Sweet Clover	✓	✓	✓
Mentha arvensis	Field Mint		✓	✓
Mentha piperita	Peppermint	✓		
Mentha spicata	Spearmint			✓
Mentha spp.	Mint	✓		
Nepeta cataria	Catnip			✓
Panicum capillare	Witchgrass	✓	✓	
Phalaris arundinacea	Reed Canarygrass	✓	✓	✓
Phleum pratense	Timothy Grass	✓	✓	✓
Physalis heterophylla	Ground Cherry		✓	✓
Poa compressa	Canada Blue Grass	✓	✓	

Poa pratensis	Kentucky Bluegrass	✓	✓	✓
Polygonum convolvulus	Wild Buckwheat			✓
Polygonum pensylvanticum	Pinkweed		✓	
Polygonum persicaria	Lady's Thumb			✓
Potentilla argentea	Silvery Cinquefoil	✓	✓	✓
Potentilla recta	Sulphur Cinquefoil	✓	✓	✓
Rosa spp.	Wild Rose	✓	✓	✓
Rubus spp	Raspberry	✓	✓	✓
Rumex acetosella	Common Sheep Sorrel	✓		✓
Rumex crispus	Curled Dock	✓	✓	✓
Satureia vulgaris	Wild Basil	✓		
Sinapis arvensis	Wild Mustard		✓	✓
Sisymbrium altissimum	Tumbleweed Mustard		✓	✓
Sisyrinchium montanum	Common Blue-Eyed-Grass	✓	✓	✓
Solidago canadensis	Canada Goldenrod	✓	✓	✓
Solidago juncea	Early Goldenrod	✓	✓	✓
Solidago nemoralis	Old-Field Goldenrod	✓	✓	✓
Solidago stricta	Narrow-leaf Goldenrod	✓	✓	✓
Solidago uliginosa	Bog Goldenrod	✓		
Solidago spp.	Goldenrod	✓		
Taraxacum officinale	Common Dandelion	✓	✓	✓
Trifolium aureum	Yellow Clover	✓	✓	✓
Trifolium pratense	Red Clover	✓	✓	✓
Trifolium repens	White Clover		✓	✓
Urtica dioica	Stinging Nettle			✓
Vicia americana	American Vetch			✓
Vicia cracca	Bird/Cow Vetch	✓	✓	✓
Vicia tetrasperma	Slender Vetch			✓
Viola spp.	Violet	✓	✓	
Betula spp.	Birch spp.		✓	✓
Betula alleghaniensis	Yellow Birch	✓		
Betula papyrifera	White Birch	✓		✓
Cornus spp.	Dogwood	✓	✓	✓
Crataegus spp.	Hawthorne spp.	✓	✓	✓
Fraxinus americana	White Ash	✓	✓	✓
Fraxinus pennsylvanica	Red Ash	✓	✓	✓
Fraxinus pennsylvanica var. subintegerrima	Green Ash	✓	✓	
Lonicera spp.	Honeysuckle Shrub	✓	✓	✓
Malus spp.	Apple spp.	✓	✓	✓
Malus spp.	Crabapple spp.		✓	✓
Populus deltoides	Eastern Cottonwood		✓	
Populus grandidentata	Large Tooth Aspen	✓		
Populus tremuloides	Quaking Aspen	✓	✓	
Prunus avium	Sweet Cherry	✓	✓	✓
Prunus pensylvanica	Pin Cherry	✓		✓
Prunus virginiana	Choke Cherry	✓	✓	✓

Quercus alba	White Oak	✓		✓
Quercus bicolor	Swamp White Oak	✓		
Quercus macrocarpa	Bur Oak	✓	✓	✓
Quercus spp.	Oak spp.	✓		
Salix discolor	Pussywillow	✓		
Salix sp. A	Willow sp. A	✓	✓	✓
Salix sp. B	Willow sp. B	✓	✓	
Spiraea latifolia	Meadowsweet	✓	✓	✓
Viburnum lentago	Nannyberry	✓	✓	✓
Viburnum rafinesquianum	Downy Arrowwood	✓		
Average species richness/site		**33**	**36**	**29**

Appendix D: Butterfly adult food plants based on the pool of all butterflies found in this study.

Scientific Name	Common name	control	forage	cash
Achillea millefolium	Yarrow	✓	✓	✓
Agrimonia spp.	Agrimony		✓	
Anaphalis margaritacea	Pearly Everlasting	✓	✓	✓
Anemone canadensis	Canada anemone	✓	✓	✓
Amelanchier laevis	Juneberry	✓		
Aquilegia canadensis	Wild Columbine	✓		
Arctium minus	Lesser Burdock		✓	✓
Arenaria serpyllifolia	Thyme-Leaved Sandwort	✓		
Artemisia absinthe	Common Wormwood		✓	✓
Asclepias incarnata	Swamp Milkweed		✓	
Asclepias syriaca	Common Milkweed	✓	✓	✓
Aster spp.	Wild Aster	✓	✓	✓
Berteroa incana	Hoary Alyssum		✓	✓
Bromus inermis	Smooth Brome Grass	✓	✓	✓
Campanula rotundifolia	Harebell	✓		
Capsella bursa-pastoris	Shepherd's Purse			✓
Chrysanthemum leucanthemum	Oxeye Daisy	✓	✓	✓
Cichorium intybus	Chickory		✓	
Cirsium spp.	Thistle	✓	✓	✓
Convolvulus sepium	Field Bindweed	✓	✓	✓
Daucus carota	Queen Anne's Lace	✓	✓	✓
Dianthus sp.	Carnation	✓		✓
Echium vulgare	Viper's Bugloss	✓	✓	✓
Epilobium hirsutum	Hairy Willow-Herb		✓	
Erigeron annuus	Daisy Fleabane	✓	✓	✓
Erigeron philadelphicus	Philadelphia Fleabane	✓	✓	✓
Eupatorium maculatum	Rough Joe-Pye Weed	✓	✓	✓
Fragaria virginiana	Virginia Strawberry	✓	✓	✓
Galium spp.	Bedstraw	✓	✓	✓
Gentiana andrewsii	Prairie Gentian	✓		
Geum aleppicum	Yellow Avens	✓	✓	✓
Glechoma hederacea	Creeping Charlie			✓
Hemerocallis flava	Yellow Daylily			✓
Hieracium aurantiacum	Orange Hawkweed	✓	✓	✓
Hieracium pilloselloida	Yellow Hawkweed	✓	✓	✓
Hypericum perforatum	Common St. Johnswort	✓	✓	✓
Inula helenium	Elecampane			✓
Ipomoea lacunosa	Pitted Morning-Glory	✓	✓	✓
Lilium philadelphicum	Wood Lily	✓		

Linaria vulgaris	Butter-and-Eggs	✓	✓	✓
Lonicera spp.	Honeysuckle Vine	✓	✓	✓
Lotus corniculatus	Birdsfoot Trefoil	✓	✓	✓
Lycopus virginicus	Bugleweed	✓	✓	✓
Lythrum salicaria	Purple Loosestrife	✓	✓	✓
Malva moschata	Musk Mallow			✓
Medicago lupulina	Alfalfa (yellow)	✓	✓	
Medicago sativa	Alfalfa (purple)	✓	✓	✓
Melilotus albus	White Sweet Clover	✓	✓	✓
Melilotus officinalis	Yellow Sweet Clover	✓	✓	✓
Mentha arvensis	Field Mint		✓	✓
Mentha piperita	Peppermint	✓		
Mentha spicata	Spearmint			✓
Mentha spp.	Mint	✓		
Nepeta cataria	Catnip			✓
Oenothera macrocarpus	Evening Primrose	✓	✓	✓
Oenothera perennis	Small Sundrops	✓		
Oxalis stricta	Yellow Wood-Sorrel	✓	✓	✓
Parthenocissus quinquefolia	Virginia Creeper	✓	✓	✓
Physalis heterophylla	Ground Cherry		✓	✓
Polygonum convolvulus	Wild Buckwheat			✓
Polygonum pensylavaticum	Pinkweed		✓	
Polygonum persicaria	Lady's Thumb			✓
Potentilla argentea	Silvery Cinquefoil	✓	✓	✓
Potentilla recta	Sulphur Cinquefoil	✓	✓	✓
Prunella vulgaris	Self-Heal	✓	✓	
Ranunculus acris	Meadow Buttercup	✓	✓	✓
Rhus toxicodendron	Poison Ivy	✓	✓	✓
Rosa spp.	Wild Rose	✓	✓	✓
Rubus spp	Raspberry	✓	✓	✓
Rudbeckia serotina	Black-Eyed Susan	✓	✓	✓
Satureja vulgaris	Wild Basil	✓		
Sedum acre	Stonecrop, Gold-Moss			✓
Sedum album	White Stonecrop	✓		
Senecio pauperculus	Round-Leaved Ragwort	✓	✓	
Silene vulgaris	Bladder Campion	✓	✓	✓
Sinapis arvensis	Wild Mustard		✓	✓
Sisymbrium altissimum	Tumbleweed Mustard		✓	✓
Sisyrinchium montanum	Common Blue-Eyed-Grass	✓	✓	✓
Solanum dulcamara	Bittersweet Nightshade		✓	✓
Solidago canadensis	Canada Goldenrod	✓	✓	✓
Solidago juncea	Early Goldenrod	✓	✓	✓
Solidago nemoralis	Old-Field Goldenrod	✓	✓	✓
Solidago rugosa	Rough Goldenrod	✓		
Solidago grandifolia	Narrow-Leaf Goldenrod	✓	✓	✓

Solidago uliginosa	Bog Goldenrod	✓		
Sonchus spp.	Sow-Thistle		✓	✓
Stachys spp.	Stachys spp.			✓
Stachys palustris	Woundwort			✓
Stellaria graminea	Stitchwort	✓	✓	✓
Taraxacum officinale	Common Dandelion	✓	✓	✓
Tragopogon dubius	Common Goat's-Beard	✓	✓	✓
Trifolium aureum	Yellow Clover	✓	✓	✓
Trifolium pratense	Red Clover	✓	✓	✓
Trifolium repens	White Clover		✓	
Tripleurospermum perforata	Scentless Chamomile		✓	✓
Verbascum thapsus	Common Mullein	✓		✓
Verbena hastata	Blue Vervain		✓	✓
Veronica officinalis	Speedwell	✓	✓	✓
Vicia americana	American Vetch			✓
Vicia cracca	Bird/cow Vetch	✓	✓	✓
Vicia tetrasperma	Slender Vetch			✓
Vincetoxicum nigrum	Dog-Strangling Vine			✓
Viola spp.	Violet	✓	✓	
Vitis riparia	Riverbank Grape	✓	✓	✓
Aralia nudicaulis	Sarsparilla	✓		
Cornus spp.	Dogwood	✓	✓	✓
Crataegus spp.	Hawthorn spp.	✓	✓	✓
Malus spp. A	Apple spp.	✓	✓	✓
Malus spp. B	Crabapple spp.		✓	✓
Prunus avium	Sweet Cherry	✓	✓	✓
Prunus pensylvanica	Pin Cherry	✓		✓
Prunus virginiana	Choke Cherry	✓	✓	✓
Rhamnus frangula	Glossy-Leaved Buckthorn	✓	✓	✓
Rhus typhina	Sumac		✓	✓
Ribes cynosbati	Prickly Gooseberry		✓	✓
Sambucus canadensis	American Elderberry		✓	
Spiraea latifolia	Meadowsweet	✓	✓	✓
Symphoricarpos albus	Snowberry	✓		
Tilia americana	American Basswood	✓	✓	
Viburnum lentago	Nannyberry	✓	✓	✓
Viburnum rafinesquianum	Downy Arrowwood	✓		
Average species richness/site		**38**	**41**	**36**