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Patterns of Long-Term Population Trends of Three Lupine-Feeding Butterflies in Wisconsin

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Abstract: We monitored consecutive generations of three lupine-feeding specialist butterflies in pine-oak barrens in central Wisconsin, USA: Frosted Elfin (*Callophrys irus*), Karner Blue (*Lycaeides melissa samuelis*), and Persius Duskywing (*Erynnis persius*) during 1991–2014. We also monitored the summer generation of Karner Blues in northwestern Wisconsin. We present results on 24 sites for Frosted Elfin and Persius Duskywing, and 39 sites for Karner Blue. Land uses in sites occupied by the federally endangered Karner Blue are regulated. Economically utilized lands classified as "Shifting Mosaic" (SM) (forestry land) or "Permanency of Habitat" (PH) (rights-of-way) are afforded a lower standard of conservation results than the more favorable management expected of Reserves (R). For all three species, reserve sites had more favorable trends than permanency of habitat and shifting mosaic sites. Frosted Elfin and Persius Duskywing had more strongly negative trends in permanency of habitat than shifting mosaic, but vice versa for Karner Blue. Shifting mosaic sites added more recently to the study had negative trends, but not as strongly as longer-monitored shifting mosaic sites. Another large shifting mosaic complex (Hunter Haven), monitored in 17 years during 1995–2014 for Frosted Elfin and Persius Duskywing, had non-negative trends. Individual reserve sites also had more favorable trends than collectively for all reserve sites, including significant positive trends for Persius Duskywing and Karner Blue, and a stable trend for Frosted Elfin. Thus, land use is implicated not only for declines but also for effective conservation of these species.

Keywords: Frosted Elfin; Karner Blue; Persius Duskywing; conservation evidence; long-term trend; long-term monitoring; pine barren; habitat management; endangered species; recovery

1. Introduction

We conducted a long-term study of three sympatric butterfly species that feed only on wild lupine (*Lupinus perennis*) (Fabaceae) as larvae in Wisconsin, USA [1–4]. The Frosted Elfin (*Callophrys irus*) is of conservation concern both in Wisconsin, where it is state-listed as threatened [5], and in many other parts of its range in the eastern USA and southeastern Canada [3,4,6–18]. The eastern subspecies of Persius Duskywing (*Erynnis persius persius*) is not listed as threatened or endangered in Wisconsin, which is at the west end of its range, but is rare or extirpated throughout the remainder of its range in the northeastern USA and southeastern Canada. The Karner Blue (*Lycaeides melissa samuelis*) has the narrowest, generally east–west historic range at the northern end of lupine range, from far eastern Minnesota through the Great Lakes states and southern Ontario to New England. The only known host in the wild for Karner Blue is wild lupine [4,19,20]. This is also the presumed only host in Wisconsin for Frosted Elfin and Persius Duskywing because of their strong association as adults with wild lupine and paucity or absence of the alternate known host (*Baptisia*) in these sites [4,21–23].

The Karner Blue was federally listed as endangered in the U.S. in December 1992 due to extirpations in many parts of its range and is considered extirpated in Canada, but has never had legal protection in Wisconsin at the state level [20,24]. A federal recovery plan for the Karner Blue was approved in 2003, but many recovery activities started before then [20,25–28]. The federal listing in 1992 immediately reduced the range of legal activities (e.g., for roadside management and timber harvest) in locations occupied by this butterfly. The Habitat Conservation Plan (HCP) for Wisconsin approved in September 1999 defined the minimum legal requirements for landowners of Wisconsin Karner Blue localities [24,29]. Land uses are not required to achieve recovery of the butterfly but must meet the lesser standard that they will be activities "with consideration for the Karner Blue butterfly and its habitat" or "will not appreciably reduce the likelihood of the survival and recovery of the Karner Blue butterfly in the wild".

In the HCP, occupied sites are categorized as either "shifting mosaic" (SM) or "permanency of habitat" (PH) [24]. Shifting mosaic sites, primarily in timber management, proceed through forest succession, with the Karner Blue expected to decline as trees shade out wild lupines. However, as forested sites are cleared of trees, the Karner Blue is expected to increase in abundance in (or colonize) wild lupines regenerating in cut sites. Permanency of habitat locations, such as roadsides and powerline rights-of-way, are to be managed to remain uncanopied in ways not harmful to Karner Blues and their required resources. Many HCP activities began well before plan approval, and management activities at some sites exceed the minimum required by the HCP, so as to become "sites to feature, protect, or enhance the Karner Blue butterfly and its habitat" akin to nature reserve (R) management and recovery activities [29].

In this paper, we analyze long-term time series of abundance for these three species of co-occurring lupine-feeding butterflies in pine-oak barrens in central and northwestern Wisconsin, USA. The assessment of a butterfly's status and trend is greatly confounded by large variability among generations attributable to fluctuations in abundance due to climatic variation [30–34], and less often documented in response to parasitoid predation [35], and density-dependent functions [36,37]. As a result, long-term monitoring is necessary to distinguish trends from that background variation [38] as well as to monitor the efficacy of conservation actions [30,31,35].

In our previous analyses, Karner Blue abundance varied tremendously among generations [39–42]. We are re-visiting these trend analyses with additional years of data because longer-term abundance data can hold unexpected outcomes [38]. We do this in the context of other lupine-feeding specialist butterflies. We have previously analyzed trend for Frosted Elfin [23,34,41] but not Persius Duskywing. Furthermore, in this study we calculate trends for more years and for several additional sites.

In the analyses here, we compare trend (correlations with year) to category of conservation effort in the sites. Although selected prior to federal listing and/or HCP approval, our long-term monitoring sites represent the three management categories: shifting mosaic (SM), permanency of habitat (PH), and reserve (R) (where recovery would be expected to occur). These results should be useful for assessing these species' status and trend in Wisconsin and for evaluating efficacy of butterfly conservation methods.

2. Materials and Methods

2.1. Study Sites

Our study sites included more than 125 pine-oak barrens in central and northwestern Wisconsin (43.93–45.98° N, 89.10–92.74° W) (Figure 1), which have both trees and herbaceous flora similar to sand prairies ("sand barrens" in [43]). Wild lupine is the only member of its genus native to Wisconsin, making it easy to identify here. It grows on sandy soil primarily in barrens in central and northern Wisconsin [43]. It also grows near some rivers in southern Wisconsin, apparently outside the geographic range of our three lupine-feeding study species [1–3,5,43]. The study sites were selected for their conservation interest, i.e., those known or thought to have specialist butterflies [22,34,40,41,44]. They included conservation lands, forest reserves (some burned by wildfire prior to the study period), and rights-of-way for highways and powerlines. These study sites occurred in an extensive landscape context of forest cover, primarily in timber reserves as well as conserved land. As a result, the habitat patches are not discretely delineated. It was beyond our scope to try to define and measure habitat patch sizes. It was not possible to visit all sites each year, but we surveyed most sites multiple times both within a year and among years, and surveyed many sites in both subregions each year.

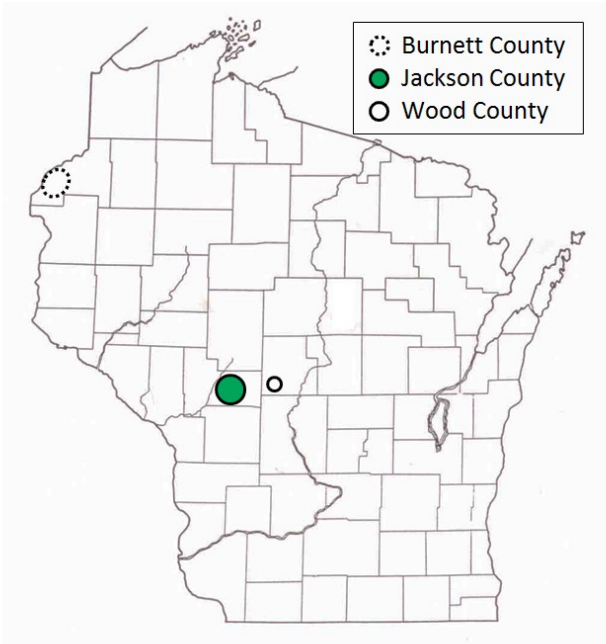

Figure 1. Map showing areas in each county containing long-term monitoring sites (Appendix A).

We did not bias toward large populations in site selection; some sites had few or no individuals detected of these three butterfly species when added to this study. Our criteria for inclusion were that the site was known to us and open to public visitation, efficient to travel to relative to sites already in the study (due to clustering of some sites and due to efficient routing among sites), appeared suitable for Frosted Elfins and/or Karner Blues, or added vegetative and management range to our sample. From this broad-scale exploration, we selected a subset of sites practical for long-term monitoring. We did not specifically target Persius Duskywing because we did not know how to do that beyond what we were already doing, but it was effectively included by our focus on the other two species.

In central Wisconsin, we started "constant-site" population monitoring (consecutive-generation surveying of a site) in two contiguous counties (Jackson, Wood) in summer 1990, and added additional monitoring sites in subsequent years (Appendix A) [40]. We had surveyed some sites in several non-consecutive generations before consecutive-generation surveying began. In northwestern Wisconsin, we consistently surveyed only in summer for Karner Blue. We started there with 11 constant sites in summer 1991 (Appendix A), with a few added in subsequent years for a total of 15 sites.

Shifting mosaic sites would be expected to afforest and decline as habitat for lupine-feeding butterflies until the next timber cutting. We attempted to recruit "new shifting mosaic" sites, starting in 2003 with one site for Frosted Elfin and Persius Duskywing monitoring (both species found). In 2006, we surveyed this site for Karner Blue too. We also added two other sites surveyed for all three species, but at only one of these two sites did we find any lupine-feeding butterflies (Karner Blue and Persius Duskywing only). Thus, our analysis here contains one new shifting mosaic site for Frosted Elfin (2003 on) and two sites from 2006 on for the other two species.

In addition, the "Hunter Haven complex" is a large block of 13 square kilometers in Jackson County Forest accessible only by forestry roads and containing extensive pine-oak barrens with lupine. We have surveyed it for Frosted Elfin and Persius Duskywing in 1995–1997, 2001, 2002 (Persius Duskywing only), and 2003 on. Due to time constraints and changeable weather, circuit length varied among survey dates, as did the number of the 22 contiguous units that we could survey within this shifting mosaic area. Since a complete survey of Hunter Haven took at least four hours and many sections of it had high forest cover, areas that we covered also varied because the weather did not remain continuously favorable for surveying cooler, shaded areas for the entire circuit. We averaged 9 km (range 3–13 km) of surveying on the peak date per year for a species, and recorded both species in all parts of this circuit. In all years in each species' time series, at least one circuit for that species had 7 km of surveying.

All long-term sites analyzed in this study have supported Karner Blue, whether we consistently monitored that butterfly there or not. Thus, all these sites were covered by federal regulation for this butterfly in some manner.

2.2. Butterfly Surveys

Frosted Elfin and Persius Duskywing have a single life cycle per year, with the adult life stage ("flight period") in spring (primarily May to early June) in Wisconsin [1–4,9,22,23,34]. The Karner Blue has two complete life cycles per year, which consist of spring and summer "broods" or adult generations [1–4,9,45]. Frosted Elfin has the earliest flight period, followed by Persius Duskywing and then the spring Karner Blue generation, but all three species overlap in the spring flight period. The summer Karner Blue generation occurs well after the end of the spring flight periods [45]. Frosted Elfin overwinters as a pupa, Persius Duskywing as a fully mature larva, and Karner Blue as an egg [2,4].

We made repeated visits to the central Wisconsin study region each year during 1991–2014 that fully covered the spring flight periods of Frosted Elfin and Persius Duskywing [34]. We also fully covered the onset and main flight period of the spring generation of Karner Blue, and the main flight period (but not necessarily start and end) of the summer generation. For Karner Blue surveying, from spring 1991 on, we did two surveys per generation during the main flight period at most if not all constant sites in central Wisconsin, plus at least one more survey date at some of these sites [40]. For Frosted Elfin and Persius Duskywing, we attempted similar amounts of repeat visits but cooler weather precluded coverage as thorough as that for Karner Blue. The goal of multiple surveys per generation was to obtain one survey as near to "peak" numbers as possible. Our surveys at other sites aided in timing surveys at monitoring sites [23,34,45]. In northwestern Wisconsin, we usually surveyed on only one date per summer for Karner Blue. Our surveying and phenological observations in central Wisconsin and elsewhere in northern Wisconsin aided in this date selection [23,34,45,46].

Frosted Elfin and Karner Blue are readily identifiable by observation without netting or handling [1,3]. However, without dissection, Persius Duskywing may only be definitively identifiable to species complex, which includes Columbine Duskywing (*Erynnis lucilius*) and Wild Indigo Duskywing (*E. baptisiae*) [3,4]. The latter two species have multiple generations per year that coincide with both the spring and summer surveys for the three lupine-feeding species. We infrequently encountered individuals phenotypically attributable to these other two duskywing species, but we did find such individuals in spring (20 and 77 individuals respectively) and summer (0 and 35 individuals, respectively). As a result, for this species complex, our identifications may not be as accurate as for Frosted Elfin and Karner Blue. However, the rarity with which we encountered duskywings in summer lends supports that Persius Duskywing is the dominant member of this species complex in our study sites. Persius Duskywing has been extensively documented with dissection in both central and northwestern Wisconsin by others [4,47].

We conducted butterfly transect surveys similar to Pollard [48] along like routes on each visit to each site [22,23,40,42,44,49]. Walking at a slow pace (about 2 km/h) on parallel routes 5–10 m apart, we counted all adult butterflies observed ahead and to the sides, to the limit an individual could be identified, with the aid of binoculars when needed, and tracked. We recorded temperature, wind speed, percent cloud cover, percent time sun was shining, route distance, and time spent surveying. Surveys occurred during a wide range of times of day and weather, occasionally in intermittent light drizzle, so long as butterfly activity was apparent, but not in continuous rain. Most peak surveys occurred within the weather parameters of the British Butterfly Monitoring Scheme [31], but in a much wider range of times of day than in the British program.

For each species, our population abundance index is the peak survey count per monitoring site per generation. We standardized this to survey distance to create an observation rate (relative abundance) per km per site. By using one peak survey during the main flight period of each generation, we avoided pseudoreplication (counting the same individual in more than one value in the dependent variable). This approach has been adequate for producing representative indices for comparisons of relative abundance within and among sites [40,42,50,51]. In instances when we had more than one count per brood, the peak count was highly correlated with the second highest count [40], indicating that our method produced robust abundance indices.

Relative abundance indices derived from transect counts (single or multiple counts per site per generation) covary strongly with estimates of absolute numbers (line-transect or mark-release-recapture), both in studies of Karner Blues [52,53] and other butterflies [48,50,54]. Relative abundance indices have the advantage of allowing more sites to be sampled in the same amount of time compared to methods for estimating absolute numbers [53]. Surveying more sites, with less effort allocated per site, generates more statistical power for detecting patterns than spending more effort in fewer sites [55]. Thus, we have maintained consistency of survey methodology and obtained the most statistical power within the limits of how much field work we could do by using the transect count method throughout our study.

Our flight period spans for Frosted Elfin are relatively rigorously documented since we found this species on our first survey of the year in known sites in only three years of the study (1997, 2004, 2006, with only one individual found on those dates) [34]. In all other years analyzed here, we surveyed known Frosted Elfin sites prior to the observed start of the flight period. The strong negative correlation of our first observed date for Frosted Elfin with spring temperature provides support for the effectiveness of our determination of the species' phenology [34]. In all years, we surveyed known Frosted Elfin sites shortly after that species' flight period ended due to our multiple survey dates during the spring Karner Blue flight period. Our observed Persius Duskywing flight period nested within those two species' flight periods, starting after Frosted Elfin and ending before we finished our spring Karner Blue surveying. We used our observations of spring Karner Blue larvae as an additional aid in predicting the start and peak of its spring flight period [45]. In addition to the two survey dates during the main flight period of each Karner Blue generation, we also surveyed on dates before and after those dates to verify the robustness of the monitoring surveys. Prior publications provided detailed itemizations of these dates [23,45]. We analyzed these observations to calculate the interval between spring and summer peak dates, including range of variation in this interval [45]. We also analyzed sex ratio so that this could also aid us in determining progress of the flight period [39]. Throughout this study, the Wisconsin Karner Blue HCP development and implementation teams maintained a network of timely sharing of Karner Blue observations in Wisconsin (absence, presence, and numbers seen). Throughout the study, we both contributed observations and benefitted from others'. The strongly significant positive correlation of our Karner Blue time series of abundance with those from Fort McCoy (in Monroe County, adjacent to our central Wisconsin study area), provides evidence for the effectiveness of our surveying to represent the relative variation in Karner Blue abundance in our study sites [40,42]. For each generation of each study species, we surveyed on more dates in order to determine the main flight period and obtain the one survey value per site per generation analyzed here.

2.3. Statistical Analyses

All analyses were done with ABstat 7.20 software (Anderson-Bell Corp., Parker, CO, USA) [56]. Statistical significance was set at two-tailed $p < 0.05$. Since significant results occurred at a frequency well above that expected due to spurious Type I statistical error, the critical p value was not lowered further, as more Type II errors (biologically meaningful patterns lacking statistical significance) would be created than Type I errors eliminated.

We used non-parametric statistical tests because these require no assumptions about whether the data are distributed normally. We used the Spearman rank correlation for correlations and the Mann–Whitney U test to test for significant differences in relative butterfly abundance among groups. We calculated trends (correlation of a species' abundance with year) by site type: reserve, shifting mosaic, permanency of habitat, new shifting mosaic sites, Hunter Haven (also shifting mosaic), and individual reserve sites.

We controlled for annual variation in weather by limiting the sample in each statistical test to sites surveyed in the same years and minimizing missing values. We analyzed different sets of shifting mosaic sites separately because of the different number of years those sites were surveyed: shifting mosaic (1994–2014, no missing values), new shifting mosaic (2003–2014 for Frosted Elfin, 2006–2014 for the other two species, no missing values), and Hunter Haven (1995–2014 but with some years missing and with variation among years in how many and which units were surveyed). The sample for reserve sites at Crex Meadows in northwest Wisconsin spans 1991–2014 with only three missing values in 1996. We chose relatively simple, widely used statistical analysis because of the relatively large number of sites and years in our samples, no missing values in most samples, and negligible missing values in the few remaining samples. Our goal was the greatest transparency and accessibility in sharing our results with other surveyors and managers, who would certainly be familiar with long-standing methods of analyzing correlations but not necessarily with more specialized or newer models specific to analyzing butterfly trends.

3. Results

3.1. Summary Statistics

On our peak surveys at the long-term monitoring sites (including new shifting mosaic), we recorded 301 Frosted Elfin individuals in 321.5 km of surveying, 860 Persius Duskywing individuals in 331.0 km of surveying, and 19,520 Karner Blue individuals in 836.1 km of surveying (both central and northwest Wisconsin). On our peak surveys in the Hunter Haven complex, we recorded 246 Frosted Elfin individuals in 146.1 km of surveying and 264 Persius Duskywing individuals in 166.1 km of surveying.

3.2. Abundance over Time

Long-term time series are illustrated in Figures 2–4, A1–A10. For each species, reserve sites had the most favorable trend compared to both permanency of habitat and shifting mosaic sites (Table 1, Figures 2–4). Only Persius Duskywing reserve sites had a non-negative trend (positive but far from significant) (Table 1). All other tests were negative to some degree. Frosted Elfin trend in reserve sites was nearly significantly negative (Table 1). Karner Blue summer trend was significantly negative in northwest Wisconsin reserve sites (Table 1). Karner Blue trend (both spring and summer generations) was non-significantly negative in central Wisconsin reserve sites (Table 1).

Frosted Elfin and Persius Duskywing had more strongly negative trends in permanency of habitat than shifting mosaic, but vice versa for Karner Blue (Table 1). The more recently added shifting mosaic sites (surveyed for a shorter period of time) also had negative trends (Figures A1–A3; Table 2), but not as strongly (as evidenced by degree of significance) as the longer-monitored shifting mosaic sites (Table 1). However, the only new shifting mosaic site where we found Frosted Elfins had a strongly negative correlation coefficient for that species (Table 2).

Table 1. Trend (Spearman rank correlation coefficients (r) of abundance vs. year) per species at the long-term monitoring sites in the central (1994–2014) and northwestern (1991–2014) subregions, at the site scale, grouped by categories of conservation effort. N = number of sites × number of years in each sample. P = category of significance of correlation.

Species	Reserve			Permanency of Habitat			Shifting Mosaic		
	N	r	P	N	r	P	N	r	P
Frosted Elfin	126	−0.150	<0.10	84	−0.509	<0.0001	147	−0.317	<0.01
Persius Duskywing	105	+0.073	>0.10	105	−0.437	<0.0001	147	−0.2430	<0.01
Karner-central									
both broods	84	−0.189	<0.10	168	−0.457	<0.0001	168	−0.757	<0.0001
spring only	42	−0.182	>0.10	84	−0.466	<0.0001	84	−0.772	<0.0001
summer only	42	−0.166	>0.10	84	−0.469	<0.0001	84	−0.763	<0.01
Karner-northwest									
Summer	260	−0.220	<0.01						

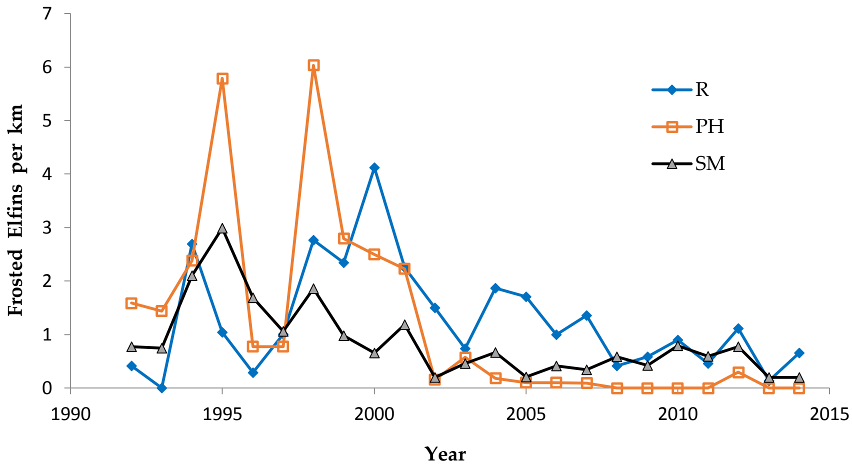

Figure 2. Mean Frosted Elfin individuals per km at the long-term monitoring sites in central Wisconsin, by site type: R = reserve (six sites), PH = permanency of habitat (four sites), SM = shifting mosaic (seven sites). Some values are missing 1992–1993; no values missing 1994–2014.

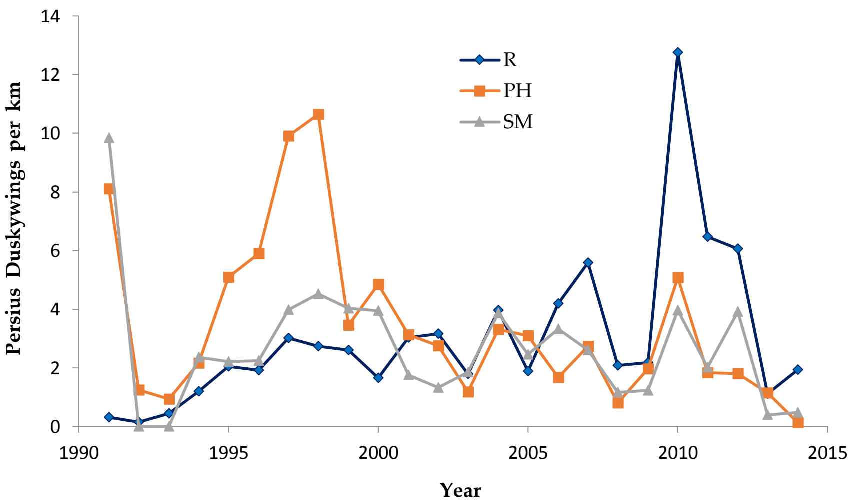

Figure 3. Mean Persius Duskywing individuals per km at the long-term monitoring sites in central Wisconsin, by site type: R = reserve (five sites), PH = permanency of habitat (five sites), SM = shifting mosaic (seven sites). Some values are missing 1991–1993; no values missing 1994–2014.

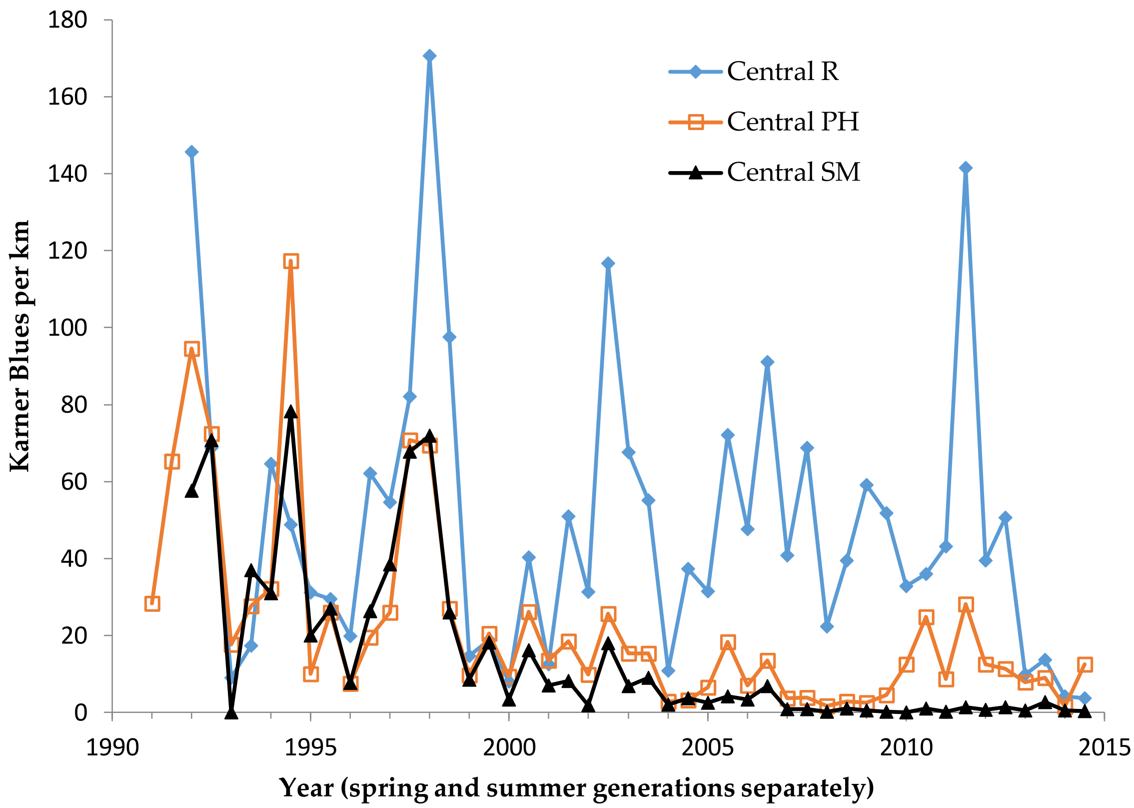

Figure 4. Mean Karner Blue individuals per km at the long-term monitoring sites in central Wisconsin, by site type: R = reserve (two sites), PH = permanency of habitat (four sites), SM = shifting mosaic (four sites). Spring brood data points are directly above the tick mark for a year, and summer brood data are between there and the next year's tick mark. No values are missing from spring 1994 through summer 2014.

The Hunter Haven complex (also shifting mosaic) had non-negative trends (far from significant) (Figures A1 and A2; Table 2). However, data from this large area were only available for Frosted Elfin and Persius Duskywing. This area had the most favorable shifting mosaic trends for these two species. In contrast to the other monitoring sites, our surveying in the Hunter Haven complex had some missing years and variation in which parts were surveyed each year.

Table 2. Trend (Spearman rank correlation coefficients (r) of abundance vs. year) per species at two new Shifting Mosaic sites (new SM), the Hunter Haven complex (SM), and Bauer-Brockway (R = Reserve). N = number of sites × number of years in each sample. P = category of significance of correlation.

Species	New SM Sites			Hunter Haven (SM)			Bauer-Brockway (R)		
	N	r	P	N	r	P	N	r	P
Frosted Elfin	12	−0.462	>0.10	16	+0.282	>0.10	68	+0.067	>0.10
Persius Duskywing	18	−0.215	>0.10	17	+0.150	>0.10	68	+0.407	<0.01
Karner central									
both broods	36	−0.419	<0.05				46	+0.327	<0.05
spring	18	−0.438	<0.10				23	+0.259	>0.10
summer	18	−0.457	0.06				23	+0.452	<0.05

Individual reserve sites also had more favorable trends (Figures A5 and A6, Tables 2 and 3) than collectively for all reserve sites (Figures 2–4; Table 1). Bauer-Brockway had significant positive trends for Persius Duskywing and Karner Blue, and a stable trend for Frosted Elfin (Table 2). The corner unit at Crex Meadows had a near-significant positive trend for Karner Blue (Table 3), in contrast to the significantly negative trend collectively in the entire sample of reserve sites from that subregion (northwest Wisconsin) (Table 1).

Among sites surveyed for all three species, the last year observed was significantly earlier for Frosted Elfin than the other two species (Table 4), and near significantly earlier for Persius Duskywing compared to Karner Blue.

Table 3. Trend (Spearman rank correlation coefficient (r) of abundance vs. year) for summer Karner Blue at the Crex Meadows corner unit (reserve) in northwestern Wisconsin. N = number of sites × number of years in each sample. P = category of significance of correlation.

Species and Brood	N	r	P
Karner Blue (summer)	24	+0.374	<0.10

Table 4. Pair-wise Mann–Whitney U tests of differences in the last year observed at 20 sites in central Wisconsin where all three species were found in this study. Since *p* values are one-tailed, significance is set at $p < 0.025$.

Species Pair	One-Tailed *p* Value	Mean Last Year	Median Last Year
Frosted Elfin		2007	2010
to Persius Duskywing	0.0024	2012	2013
to Karner Blue	<0.0001	2013	2014
Persius Duskywing			
to Karner Blue	0.0266		

4. Discussion

4.1. Status and Trend in Wisconsin

These population trends result from both the happenstance of annual fluctuations at the start and end of the study period as well as true long-term trends related to directed patterns in both habitat (vegetation and management) and climate (see Introduction). It is unclear how much these trends are due to climate and how much could be addressable by land managers. Thus, the results of this study are more meaningful as relative comparisons among species and types of conservation effort.

Of the study species, Frosted Elfin is the most restrictive and most in decline, based on the last year observed (number of known extant sites) (Table 4). However, the most abundant of the study species (Karner Blue) shows some of the steepest declines in abundance trends (Table 1). A greater level of conservation protection (in reserve sites) ameliorated the abundance trend for all three species. It is unclear how much of that was due to conservation efforts targeting what were already known to be the best sites for protection, and how much is due to differences in conservation management strategies. However, afforestation in shifting mosaic sites and more lenient management guidelines in permanency of habitat sites both associate with steeper declines. Our small sample of "new" shifting mosaic sites also shows negative trends (Table 2).

The species whose habitat more often includes very open habitat (Karner Blue) was the only one with a relatively weaker statistical pattern of negative trend in permanency of habitat sites (which are open rights-of-way) than shifting mosaic sites (Table 1). However, the negative overall trend at permanency of habitat sites for Karner Blue suggests that permanency of habitat sites are not successful overall at being "permanent" (i.e., stable) habitat. Species more tolerant of forested habitat (Frosted Elfin especially and also Persius Duskywing) had a relatively weaker statistical pattern of negative trends in shifting mosaic (forestry) sites than in permanency of habitat sites.

These results are consistent with our prior assessment of the long-term trend of the five species of elfins in central Wisconsin [34]. In that analysis, Frosted Elfin significantly declined overall while the two other specialist elfins increased significantly and two generalist elfins had stable trends. Two specialists (including Frosted Elfin) and one generalist had more favorable trends in reserve than shifting mosaic and permanency of habitat. However, Frosted Elfin declined in all categories, significantly so in shifting mosaic and permanency of habitat and non-significantly in reserve.

However, in this analysis, the Hunter Haven complex (shifting mosaic) shows promise since the trends for the two testable species (Frosted Elfin, Persius Duskywing) were non-negative there (Table 2). This suggests that shifting mosaic guidelines can be implemented in ways that are compatible with conservation objectives. However, the large size of this block of land and the low intensity of land use there are also likely factors contributing to the trends here [14,22,41].

Another encouraging result comes from the specific examples of individual sites (Tables 2 and 3). These were outstanding sites at the outset and were targeted for reserve management. They had positive or neutral trends for all species, compared to negative trends collectively for groups of sites. Likewise, for Karner Blue at Fort McCoy in central Wisconsin, Guiney et al. [36] found non-declining, stably synchronous fluctuations at 7 of 11 sites in 12 generations from spring 1998 to summer 2003.

4.2. Land Use and Management Studies

Conservationists should apply lessons from sites with relatively better population trends to understand what habitat and land-use factors may help maintain those specialists more successfully in the long-term. A seven-year study monitored a lupine-feeding population of Frosted Elfin in New York state both before and after selective pine tree removal [14]. Both lupine cover and elfin usage increased significantly in the openings. In a Wisconsin site with native prairie mammal herbivory [57], Karner Blues positively associated with areas of greater usage by bison (*Bison bison*) as evidenced by droppings and wallows. Bison activities reduced woody growth, and wild lupine was significantly disassociated with shrubs and trees. Another deliberate conservation for both Karner Blue and Frosted Elfin is the permanent non-fire refugium, as previously reported and still on-going at both Bauer-Brockway Barrens and the corner unit at Crex Meadows (Tables 2 and 3; Figures A5 and A6) [41]. Thom and Daniels [18] found a positive relationship for lupine-feeding Frosted Elfin with duff and litter. While this could be a stand-in for time since the last dramatic, soil-baring land use event (fire, soil scarification) [22,41,44], it could also indicate the need for these resources either directly (suitable microclimate for larvae) or indirectly, such as improving moisture content of the host plant. This factor has also been identified for Karner Blue [36]. Regardless of the underlying mechanism(s), it appears that Frosted Elfin needs "mature" habitat (with long periods since last dramatic management) that is nonetheless open enough to support abundant lupine.

Walsh [58] reported on the climatic bottleneck of extreme heat and drought in spring and summer 2012 in the Great Lakes region. Sites in Ohio for Karner Blue re-introduction had the highest heat load (an index of incidental solar radiation adjusted for differences in aspect, slope, and elevation but not structures or vegetation). All of these populations failed following 2012, except for a population naturally established by colonization from a release site. Occupied sites in Michigan were intermediate in heat load, while formerly occupied sites in Michigan had the lowest heat load but highest canopy (afforestation). Thus, conservation land management must not only maintain suitable vegetative characteristics by preventing excessive canopy, but must also maintain climate-resilient refugia from climatic extremes.

The conservation concern for these species in both Canada and the United States (see Introduction) has been warranted. Our long-term monitoring indicates decline for all three species in Wisconsin, as has been reported for all three species elsewhere. It is difficult to turn around broad-scale long-term landscape factors implicated in butterfly declines, and land use is strongly implicated as a prominent factor in butterfly decline [35]. This is evidenced in our study since the higher level of conservation management (reserve) had more favorable trends than in the long-term sites in the other management categories: shifting mosaic in forestry and permanency of habitat in rights-of-way.

Thus, land management is also likely to be a viable means to improve the status and trend of these species, since reserve sites, either collectively or at individual sites, had non-declining trends. In addition, the Hunter Haven complex (a large shifting mosaic site) also had non-declining trends, indicating the potential for economically motivated land uses to be compatible with these butterfly species' requirements long-term. Site-specific positive outcomes in both ecological and economic land uses are possible [22,34,41].

5. Conclusions

This study supports the concept of umbrella species for conservation [35]. Management guidelines and restrictions aimed at conserving the Karner Blue also benefitted other lupine-feeding butterfly species in the same sites. This is evidenced by the improved outcome in reserve than shifting mosaic or permanency of habitat for all three study species, as well as the non-declining trend for Frosted Elfin and Persius Duskywing in the Hunter Haven complex (shifting mosaic).

However, there are limits to Karner Blue as an umbrella for the other two species. For example, Karner Blue colonized plantings on former farmland, which is a notable conservation success for a localized butterfly [59]. However, this is more likely for Karner Blue [29,59] than the more habitat-restricted Frosted Elfin and Persius Duskywing. A focus combining both Karner Blue and Frosted Elfin requirements does appear quite effective at including Persius Duskywing, at least in Wisconsin. We did not deliberately target Persius Duskywing habitat requirements in study site selection, but our focus on Karner Blue and Frosted Elfin also happened to include Persius Duskywing effectively.

Supplementary Materials: The following are available online at http://www.mdpi.com/1424-2818/10/2/31/s1, Table S1: Supplementary Data File lupinedatafile.csv. This file contains seven data files: lastyear.csv contains site abbreviation (site) and the last year we recorded Frosted Elfin (lastyrfrl), Persius Duskywing (lastyrpdw), and Karner Blue (lastyrkbl); frlt.csv contains site abbreviation (site), year of survey (year), observation rate of Frosted Elfin individuals/km (frkm), and category (PH = permanency of habitat, SM = shifting mosaic, R = reserve), for long-term monitoring sites; kblt.csv contains site abbreviation (site), year of survey (year), brood (1 = spring, 2 = summer), observation rate of Karner Blue individuals/km (kblkm), category (PH = permanency of habitat, SM = shifting mosaic, R = reserve), and subregion (Central or Northwest), for long-term monitoring sites; kbnewsm.csv contains site abbreviation (site), year of survey (year), brood (1 = spring, 2 = summer), and observation rate of Karner Blue individuals/km (kblkm), for "new shifting mosaic" monitoring sites; pdwlt.csv contains site abbreviation (site), year of survey (year), observation rate of Persius Duskywing individuals/km (pdwkm), and category (PH = permanency of habitat, SM = shifting mosaic, R = reserve), for long-term monitoring sites; pdwnewsm.csv contains site abbreviation (site), year of survey (year), and observation rate of Persius Duskywing individuals/km (pdwkm), for "new shifting mosaic" monitoring sites; hh.csv contains year of survey (year), observation rate of Frosted Elfin individuals/km (frkm) and Persius Duskywing individuals/km (pdwkm), identifiers for surveys included in Frosted Elfin (frlt) and Persius Duskywing (pdlt) time series, for the Hunter Haven complex.

Author Contributions: Both authors collaborated on all aspects of the paper, and no one else contributed to the butterfly data analyzed here. A.B.S. and S.R.S. conceived and designed the study; A.B.S. and S.R.S. performed the study; A.B.S. and S.R.S. analyzed the data; A.B.S. and S.R.S. contributed the materials and analysis tools; there were no experiments; A.B.S. and S.R.S. wrote the paper.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Table A1. Long-term monitoring sites in central Wisconsin. The first three columns identify long-term monitoring sites by species monitored: F = Frosted Elfin, P = Persius Duskywing, K = Karner Blue. The fourth column identifies the site type: P = Permanency of Habitat, R = Reserve, S = Shifting Mosaic. For Frosted Elfin and Persius Duskywing, "YY prior" identifies the year(s) of surveying prior to consecutive-year long-term monitoring, "Monitor since" identifies the initial year of consecutive-year monitoring, and "Total indiv" (individuals) found on the peak survey in all years of surveying (both prior and consecutive-year monitoring). For Karner Blue, "Monitor" identifies the first generation of consecutive-generation monitoring. Key to abbreviations, latitude, and longitude are provided in Table A3. For Frosted Elfin at two sites, "(+1)" indicates an individual seen at each site but not on a formal survey.

					Frosted Elfin			**Persius Duskywing**			**Karner Blue**
Site Name And Type					**YY Prior**	**Monitor Since**	**Total Indiv.**	**YY Prior**	**Monitor Since**	**Total Indiv.**	**Monitor Since**
Jackson County											
F	P		S	Bauer 2	92	94	15	92		59	
F	P		S	Bauer 3	92	94	18	92		38	
F	P		R	Brockway 1	92	94	28	91–92		62	06 spring
F	P	K	R	Dike 17	88–89	91	4	88–89	91	28	90 summer
F	P		S	NBRE		92	13		92	37	97 spring
F	P		R	SBRW 1		92	17		92	33	95 spring
F	P	K	R	SBRW 4		92	30		92	70	92 spring
F	P	K	P	Stanton Main		92	5		91	87	91 spring
F	P	K	S	WCM 2		92	14		92	15	92 spring
F	P	K	S	WCM 4		92	13		92	67	92 spring
F	P	K	P	WCM 5	92	94	3		94	19	94 spring
F	P	K	S	WildSp NE		92	3		91	20	90 summer
F	P	K	S	WildSp SE		93	8	91	93	21	93 spring
Wood County											
F	P	K	P	Hwy X (main)		91	104		91	131	90 summer
	P	K	P	Hwy X E-W		92	0(+1)		92	73	91 spring
F	P		P	Hwy X South		93	14		93	60	95 spring
F			R	Sandhill 2	92	94	4			4	
F			R	Sandhill 3		94	1(+1)			5	
F	P	K	R	Sandhill 5	92, 94–97	09	0	92, 94–97	09	3	95 spring
	P		R	Sandhill 7		94	0		93	13	

Table A1. *Cont.*

					Frosted Elfin			**Persius Duskywing**			**Karner Blue**
Site Name And Type					**YY Prior**	**Monitor Since**	**Total Indiv.**	**YY Prior**	**Monitor Since**	**Total Indiv.**	**Monitor Since**
New Shifting Mosaic sites											
Jackson County											
	P	K	S	Lichtner			0		06	3	06 spring
F	P		S	HH complex	95–97, 01	03	246	95–97	02	264	
Wood County											
F	P	K	S	County Forest on Hwy X		03	7		03	24	06 spring
Included in “last year” analysis because we consistently surveyed the sites since each species last found:											
F	P	K	R	Bauer cut		00	5		03	24	06 spring
F	P	K	R	SBRW 5	95, 97	01	16	95, 97	01	47	01 spring

Table A2. Latitude and longitude for central Wisconsin study sites.

County and Site	N Latitude	W Longitude
Long-term monitoring sites		
Jackson County		
Bauer 2	44.3	90.775
Bauer 3	44.3	90.77
Brockway 1	44.3	90.75
Dike 17	44.31	90.564
NBRE (North Brockway East)	44.32	90.73
South Brockway West (SBRW):		
1	44.281	90.742
4	44.283	90.744
Stanton Main	44.23	90.65
West Castle Mound (WCM):		
2	44.273	90.764
4	44.27	90.77
5	44.275	90.765
Wildcat-Spangler (WildSp):		
NE	44.278	90.678
SE	44.275	90.678
Wood County		
Highway X (main)	44.34	90.13
Highway X E-W	44.3	90.13
Highway X South	44.32	90.13
Sandhill 2	44.33	90.13
Sandhill 3	44.33	90.15
Sandhill 5	44.33	90.18
Sandhill 7	44.33	90.2
New Shifting Mosaic sites:		
Jackson County		
Lichtner	44.382	90.689
Hunter Haven (HH) complex average:	44.231	90.684
Wood County		
County Forest	44.33	90.12
Included in "last year" analysis (Jackson County):		
Bauer cut	44.285	90.755
SBRW 5	44.28	90.75
Not included in any analysis (0 Frosted Elfins and only 1–5 Persius Duskywings found):		
Jackson County:		
South Brockway East	44.283	90.733
Wood County:		
Sandhill 1	44.317	90.13
Highway X SW	44.33	90.117

Table A3. Long-term monitoring sites in northwest Wisconsin, for Karner Blue in summer only. * indicates no survey could be done in 1996. The first column identifies the site type: P = Permanency of Habitat, R = Reserve, S = Shifting Mosaic.

Site Type	Site	Long-Term Unit Since (YY):	N Latitude	W Longitude
S	Burnett County Forest Peet Unit	94	45.905	92.543
P	Burnett County Forest Peet Road N	95	45.91	92.545
R	Crex Meadows James Road	91	45.877	92.5525
R	Crex Meadows Klots Road	91	45.88	92.55
R	Crex Meadows Main Refuge Road	91*	45.875	92.554
R	Crex Meadows North Refuge Road	91	45.92	92.58
R	Crex Meadows Phantom Prairie	91	45.83	92.67
R	Crex Meadows Reed Lake Road East	91	45.92	92.58
R	Crex Meadows corner	91	45.905	92.55
R	Crex Meadows overlook NE	91 *	45.88	92.632
R	Crex Meadows overlook NW	91 *	45.88	92.634
R	Crex Meadows overlook SE	91 *	45.878	92.632
R	Crex Meadows overlook SW	91	45.878	92.634
R	Stolte Road 1	98	45.738	92.74
R	Stolte Road 2	98	45.735	92.74

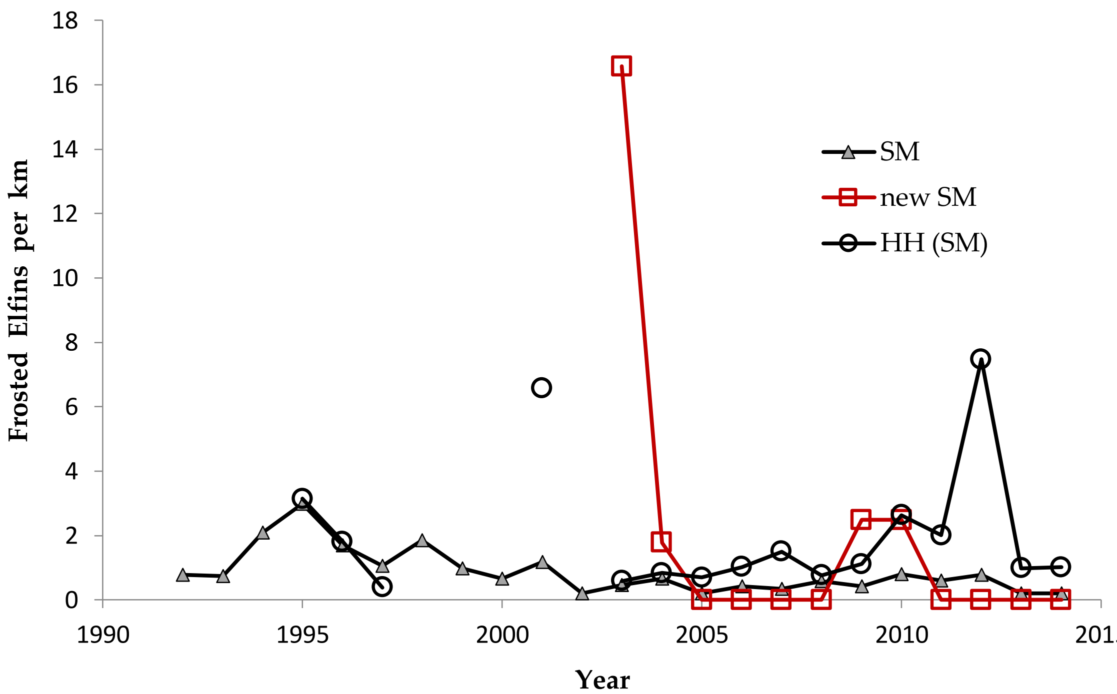

Figure A1. Mean Frosted Elfin individuals per km at the seven long-term SM (shifting mosaic) monitoring sites, and Frosted Elfin individuals per total km at the new shifting mosaic site and the Hunter Haven (HH) complex (also shifting mosaic), all in central Wisconsin. We surveyed a mean and median of 13 units (range 4–19) per year in the Hunter Haven complex.

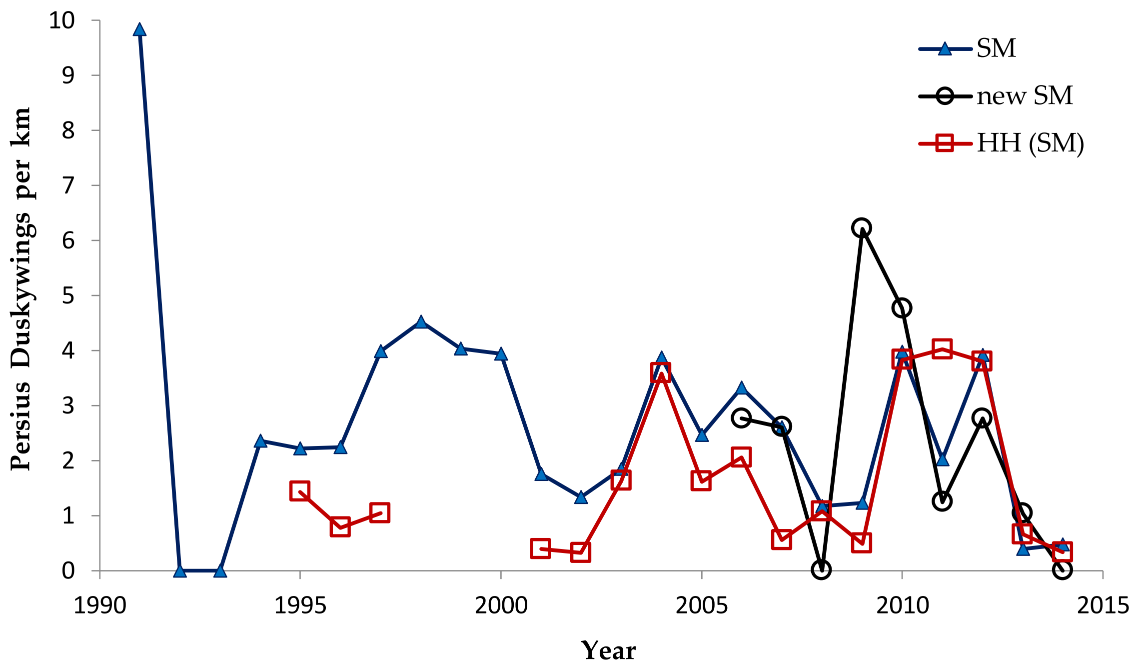

Figure A2. Mean Persius Duskywing individuals per km at the seven long-term SM (shifting mosaic) and two new shifting mosaic sites (2006–2014), and Persius Duskywings per total km per year at the Hunter Haven (HH) complex (also shifting mosaic), all in central Wisconsin. We surveyed a mean and median of 13 units (range 4–19) per year in the Hunter Haven complex.

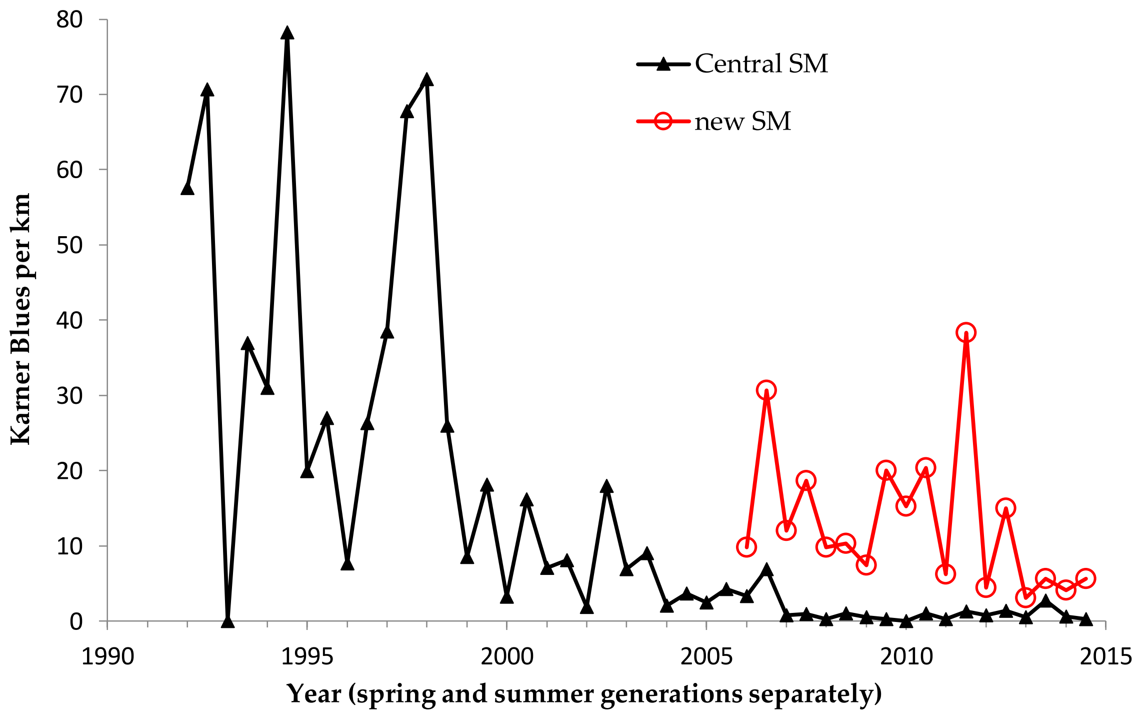

Figure A3. Mean Karner Blue individuals per km at four long-term SM (shifting mosaic) sites (spring 1994 to summer 2014) and two new shifting mosaic sites (spring 2006 to summer 2014), all in central Wisconsin. Spring brood data points are directly above the tick mark for a year, and summer brood data are between there and the next year's tick mark.

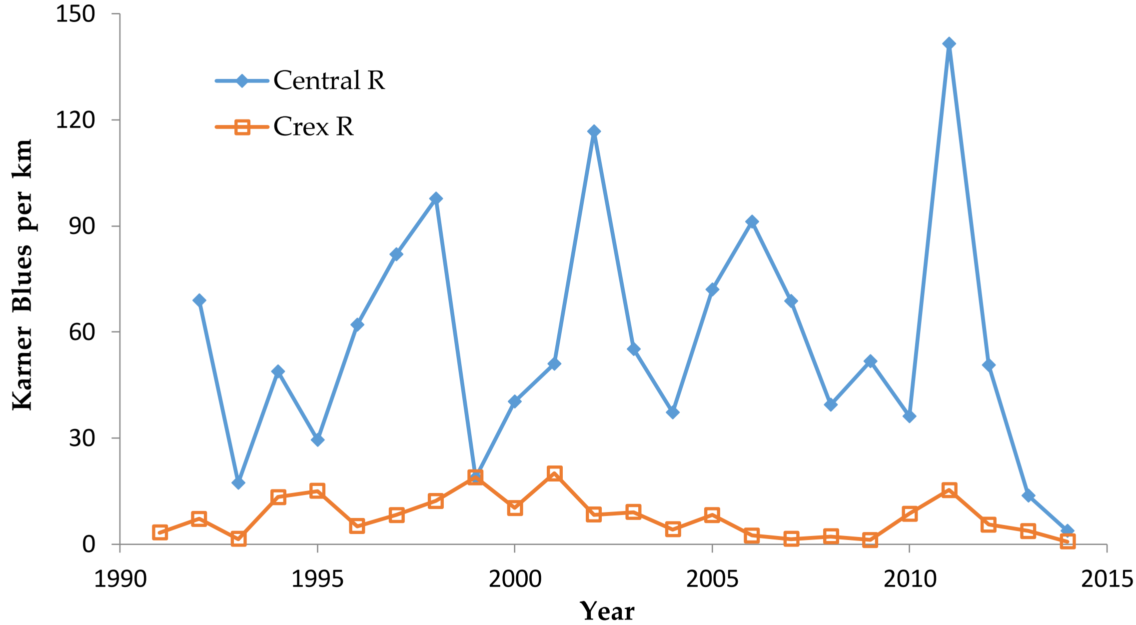

Figure A4. Mean Karner Blue individuals per km in summer at long-term R (reserve) in central Wisconsin (two sites, 1992–2014, no missing values) and at Crex Meadows in northwest Wisconsin (11 sites, 1991–2014, three missing values in 1996).

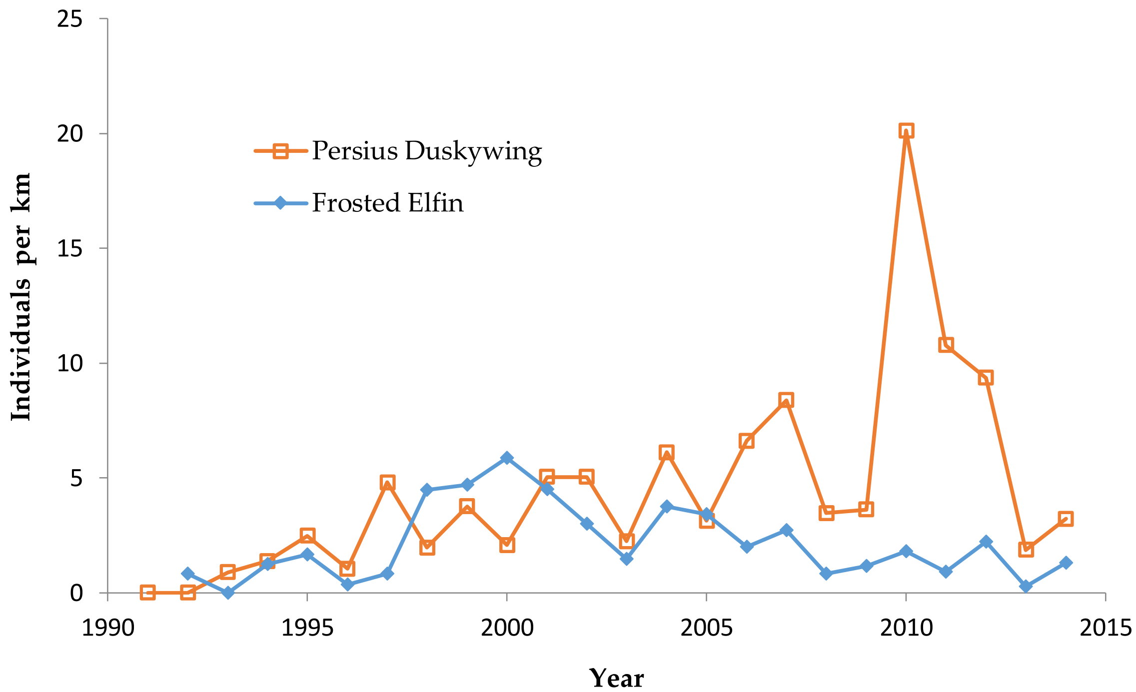

Figure A5. Mean individuals per km at three units within the Bauer-Brockway Barrens site (R = reserve) surveyed for Frosted Elfin (1992–2014) and Persius Duskywing (1991–2014). One value is missing in 1993.

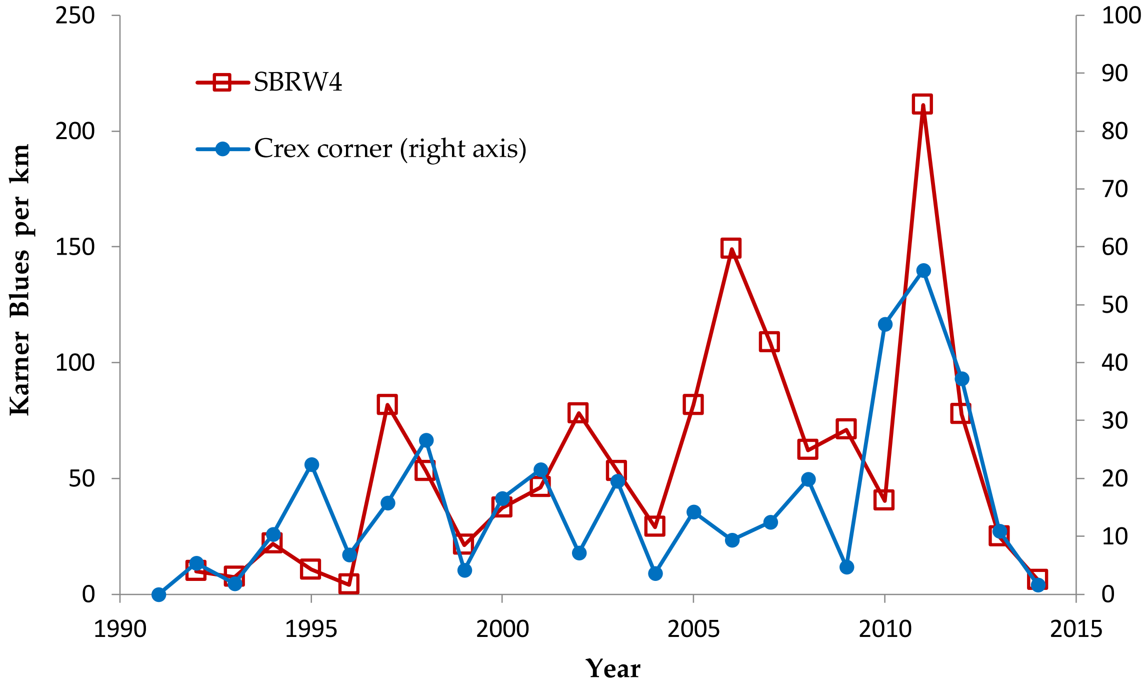

Figure A6. Karner Blue individuals per km in summer at one unit in the Bauer-Brockway Barrens site (R = reserve) in central Wisconsin surveyed each year 1992–2014 and at the corner unit (reserve) at Crex Meadows in northwest Wisconsin surveyed each year 1991–2014.

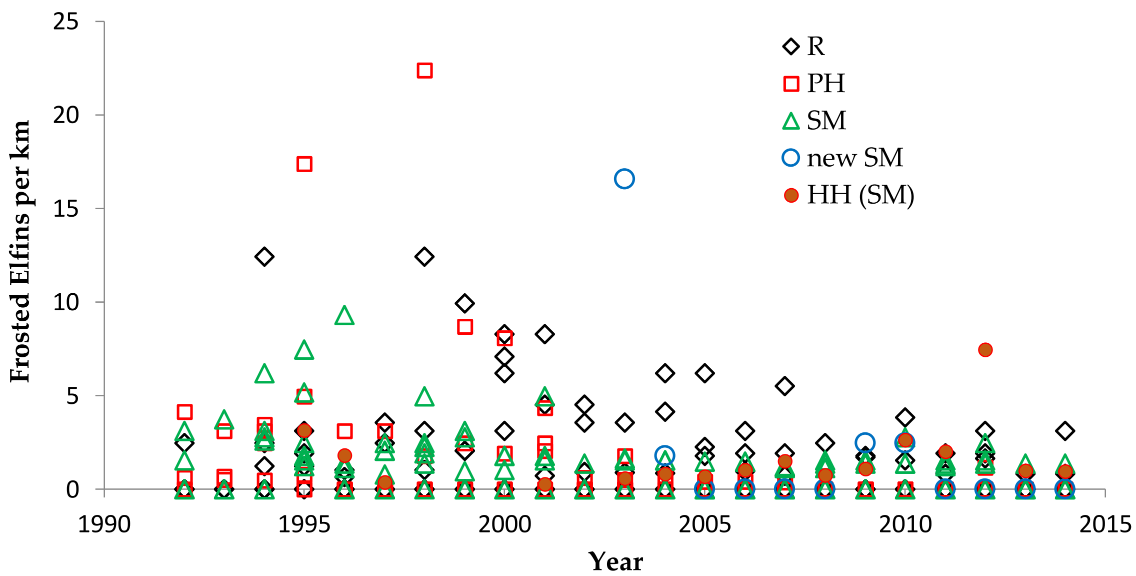

Figure A7. Scatterplot of all individual site indices used to create the mean plot points in Figures 2 and A1: Peak Frosted Elfin individuals per km at each long-term monitoring site each year in central Wisconsin, by site type: R = reserve (six sites), PH = permanency of habitat (four sites), SM = shifting mosaic (seven sites), the new shifting mosaic site, and the Hunter Haven (HH) complex (also shifting mosaic).

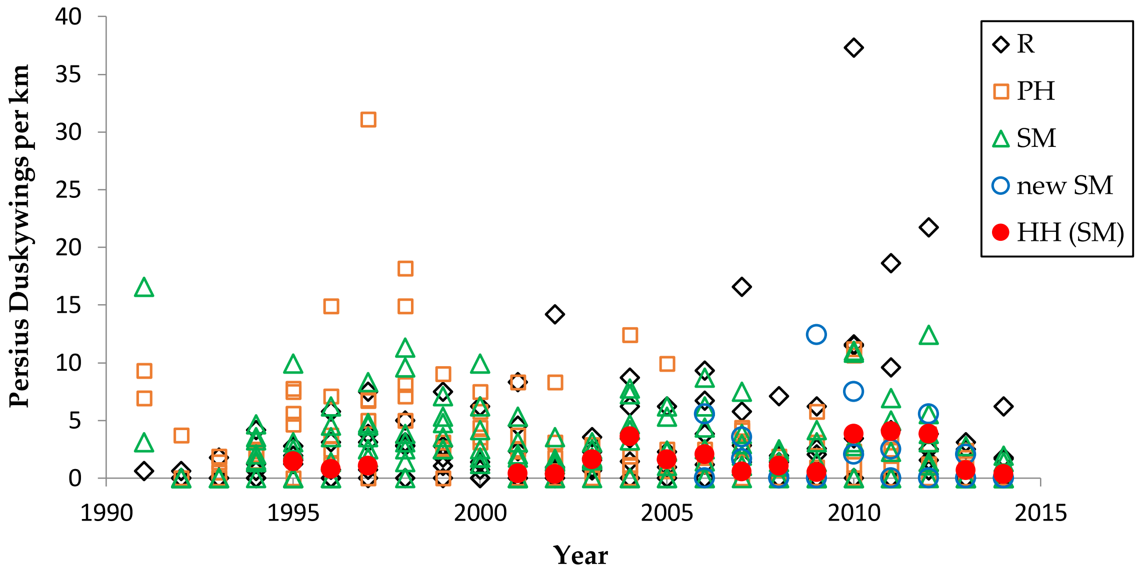

Figure A8. Scatterplot of all individual site indices used to create the mean plot points in Figures 3 and A2. Peak Persius Duskywing individuals per km at each long-term monitoring site each year in central Wisconsin, by site type: R = reserve (five sites), PH = permanency of habitat (five sites), SM = shifting mosaic (seven sites), two new shifting mosaic sites (2006–2014), and the Hunter Haven (HH) complex (also shifting mosaic).

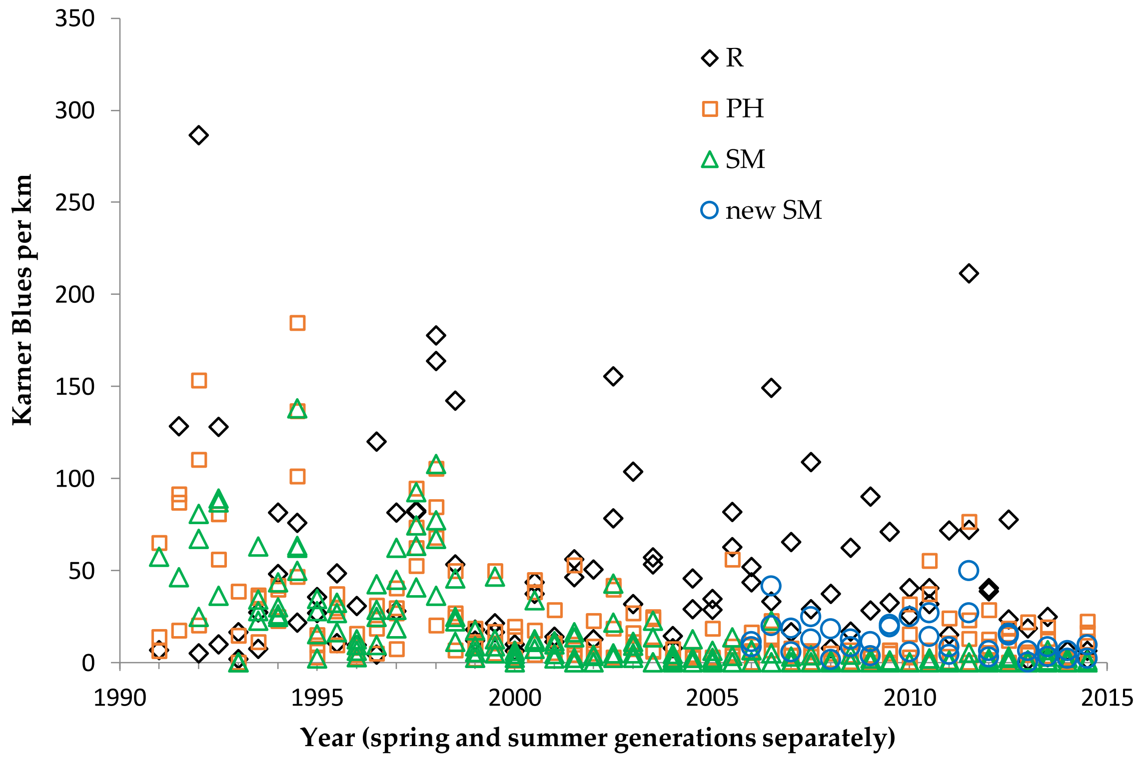

Figure A9. Scatterplot of all individual site indices used to create the mean plot points in Figures 4 and A3: Peak Karner Blue individuals per km at each long-term monitoring site each year in central Wisconsin, by site type: R = reserve (two sites), PH = permanency of habitat (four sites), SM = shifting mosaic (four sites), and two new shifting mosaic sites (spring 2006 to summer 2014).

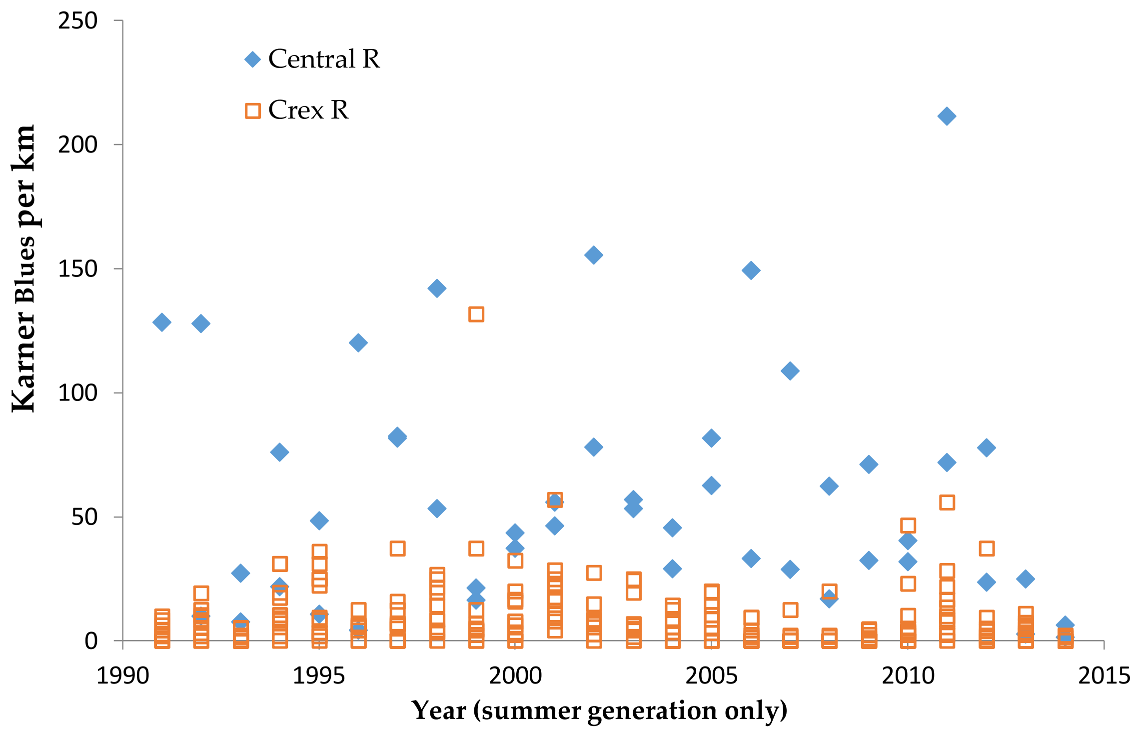

Figure A10. Scatterplot of all individual site indices used to create the mean plot points in Figure A4: Peak Karner Blue individuals per km in summer at each long-term reserve site each year in central Wisconsin (two sites, 1992–2014, no missing values) and at each Crex Meadows site in northwest Wisconsin (11 sites, 1991–2014, three missing values in 1996).

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