Landscape- and local-level variables affect monarchs in Midwest grasslands

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Abstract

Context  It is estimated that over one billion milkweed stems need to be restored to sustain the eastern North American migratory population of monarch butterflies; where and in what context the stems should be placed on the landscape is key to addressing habitat deficits.

Objectives  We assessed how the amount of appropriate habitat surrounding a particular patch of monarch habitat affects monarch presence and reproduction. To ensure that habitat restoration efforts are targeted towards areas that maximize monarch population growth, it is important to understand the effects of landscape heterogeneity on monarch occurrence in habitat patches (i.e. grasslands with milkweeds) across the landscape.

Methods  Over two summers (2018–2019), we surveyed monarch adults, larvae, and eggs at sixty grassland sites in Wisconsin that varied in patch size and landscape context (proportion grassland, forest edge density, and road density). We also estimated milkweed density and floral richness to characterize local patch quality.

Results  Adult monarch abundance was highest at patches with the lowest proportion of surrounding grassland and lowest road density, and was heavily influenced by patch quality variables. Egg and larva density in a patch increased with milkweed density and floral richness within a patch. Patch size was unrelated to monarch abundance.

Conclusions  These results suggest that optimal sites for monarch habitat restoration are within landscapes which contain little habitat and that high milkweed density and floral richness and abundance should be conservation goals.

Keywords  Monarch · Landscape · Restoration · Ecology · Local vs. landscape effects · Patch size

Supplementary Information  The online version contains supplementary material available at https://doi.org/10.1007/s10980-021-01341-4.
Introduction

Human activities, predominantly the expansion of industrialized agriculture, have simplified landscapes globally. Temperate grassland biomes and their biodiversity are particularly at risk from this intensification due to habitat loss, fragmentation, and degradation in quality (Hoekstra et al. 2005). These anthropogenic changes in landscape structure are thought to be related to widespread declines of insects that depend on grasslands and other non-agricultural habitats (Hallmann et al. 2017) and the negative effects on grassland butterfly communities are well documented (Habel et al. 2019; Wepprich et al. 2019). In addition to the effects of agricultural intensification on landscape structure and isolation, we also know that a decline in habitat quality (e.g. host plant density, floral species richness and abundance) has strong effects on butterflies (Wepprich et al. 2019). Habitat degradation and structural changes to landscapes means that there are many factors simultaneously influencing spatial patterns in butterfly occurrence and abundance.

One factor that often influences butterfly abundance is the size of a patch of breeding habitat, however, the directionality of this effect varies based on species. Established theory suggests larger patches are better at supporting specialist lepidopteran populations (Root 1973; Hill et al. 1996; Öckinger and Smith 2006). If key habitat in the landscape is rare, small isolated habitat patches surrounded by non-habitat create landscapes that should on the whole be generally unfavorable for insects. However, there is evidence that small patches can facilitate higher immigration rates than large patches for some butterfly species thus allowing for greater persistence at the landscape scale (Schultz and Crone 2008). In other cases, occupancy probability is similar for small and large patches, but as patch isolation increases, large patches have a higher likelihood of occupancy (Matter et al. 2005). Equivocal evidence from previous studies highlights the need to elucidate the relative importance of patch size and patch isolation on butterfly abundance at a species level, and interactions between patch size and isolation. Additionally, the uncertain roles of patch size and landscape-level habitat composition on the abundance of species raises the question of whether differences in dispersal behavior may account for the different responses of butterflies to these factors.

Species that are strong dispersers may be less sensitive to area-based effects because of their capacity to easily find dispersed patches in a landscape (Hill et al. 1996; Ducatez et al. 2014).

In addition to habitat patch size and isolation, it is well understood that habitat quality can influence whether butterflies will utilize a habitat patch. For example, at a community scale, butterfly assemblage structure is driven by floral abundance and richness, as nectar is the primary energy source for adult butterflies (Potts et al. 2009). Butterfly abundance is also tightly linked with host plant density (Pleasants and Oberhauser 2013; Curtis et al. 2015). Thus, the effects of local habitat quality can be an important determinant of butterfly abundance, and this effect can interact with host plant availability at broader scales (Thomas and Hanski 1997).

We studied the eastern North American migratory subpopulation (hereafter “population”) of monarch butterflies (Danaus plexippus). We performed a 2-year study in the Upper Midwestern USA (Wisconsin) to examine how habitat availability at different spatial scales (patch-level and broader landscape-scale) interacts with local patch quality to influence butterfly abundance. Both milkweed density (Pleasants and Oberhauser 2013) and the diversity and abundance of flowering plants (Potts et al. 2009) influence monarch use of patches. Breeding habitat for monarchs requires milkweed plants (Asclepias spp.), the host plants of monarch larvae, and additional flower nectar resources used by adult butterflies. As a specialist migratory species, monarchs are associated with patchy habitat in landscapes and respond to the quality of a patch, making them an ideal study species to assess the effects of both landscape- and local-scale characteristics. Yet, for these strong fliers that migrate northwards into their summer breeding grounds in the upper Midwestern U.S. (Oberhauser and Solensky 2004), the relative role of landscape scale habitat compared to local patch characteristics is not known and the determinants of habitat use could be different than for many other butterfly species whose population dynamics are mostly influenced by local dynamics (Thomas et al. 2001). To our knowledge, our study is the first to analyze the joint effects of landscape and patch characteristics on monarch abundance on a spatial scale relevant to this mobile species.

As strong fliers, it is possible that monarchs could move across the landscape in a way that would make
them largely unaffected by the amount of grassland habitat, and that densities of butterflies within a grassland patch would be independent of the amount of grassland in the surrounding landscape. On the other hand, patches of grassland habitats situated in landscapes containing a greater amount of additional grassland area might have relatively greater monarch abundance due to longer retention of monarchs in such landscapes (Zalucki and Kitching 1982; Zalucki 1983) and an increase in the likelihood of spillover from nearby habitat patches (Grant et al. 2018). While little is known about how monarchs locate or choose habitat patches, studies investigating the effect of patch size indicate that larger patches contain more monarch adults (Davis et al. 2007; Dinsmore et al. 2019). On the other hand, simulations by Grant et al. (2018) suggest that establishing many small patches of habitat, rather than few large patches, will yield the highest numbers of eggs laid by individual monarchs. This result suggests that both patch size and the distribution of patches on the landscape contribute to monarch abundance. However, there are currently no empirical data to test the hypothesized relationship between monarch abundance and landscape at a spatial scale relevant to monarch migratory abilities.

Thus, we hypothesized that landscape-level habitat characteristics would have some effect on monarch abundance at a patch, but the directionality of this effect was uncertain. We also hypothesized that monarch density would be inversely related to patch size, with higher density in small patches, in accordance with models suggesting that small patches are more valuable for monarch recruitment (Zalucki et al. 2016; Grant et al. 2018). Finally, we hypothesized that local patch-level characteristics would interact with broad-scale landscape characteristics to influence monarch abundance (Tschamntke et al. 2002; Davis et al. 2007; Grant et al. 2018). For example, although small grassland habitat patches may generally have higher monarch densities than large patches, colonization of these small patches may be dependent on the amount of surrounding grassland in the landscape, with small patches benefiting more from greater potential source populations in the landscape than large patches.

Understanding the influence of patch and landscape characteristics on monarchs will lead to improved recommendations for management of this butterfly species, as well as others with similar natural history characteristics (Brudvig 2011). In turn, this clearer understanding of the ecological effects of the loss and degradation of grassland ecosystems can serve to improve restorations for diverse and abundant assemblages of butterflies.

**Methods**

**Monarch ecology & natural history**

As a migratory species, the monarch butterfly population travels from their overwintering grounds in Mexico to breeding habitat in the U.S. and Canada in early spring. The timing of the butterflies’ arrival in the Upper Midwest varies annually based on weather as they move northward, populating North America in waves as they colonize patches of habitat (Walton et al. 2005). Monarchs are usually first sighted in Wisconsin in early- to mid-May (Howard and Davis 2015), where they can be found using any of Wisconsin’s twelve native species of milkweed as host plants. Some research suggests that monarchs show a preference for rose milkweed, *A. incarnata* (Pocius et al. 2018), but evidence of monarch preference for oviposition across milkweed species is generally scant.

Twenty years ago, a significant proportion of monarchs originating in the Upper Midwest utilized milkweed found in agricultural habitats (Oberhauser et al. 2001). Since the introduction of genetically modified herbicide-tolerant row crops, milkweed within crop fields has largely disappeared, significantly reducing the availability of monarch host plants in agricultural settings (Pleasants and Oberhauser 2013; Thogmartin et al. 2017c; Stenoien et al. 2018). The loss of summer breeding habitat has been implicated as an important driver of the decline (Pleasants and Oberhauser 2013; Pleasants 2017; Thogmartin et al. 2017c; Saunders et al. 2018), as have weather-related and other factors that are likely to affect monarch survival and reproduction throughout their migratory cycle (Altizer and Oberhauser 1999; Oberhauser 2012; Thogmartin et al. 2017c; Saunders et al. 2018). Demographic analyses suggest that adding milkweed in the upper Midwestern U.S. will have a large impact on the monarch population (Oberhauser et al. 2017). Recent estimates of the extent of habitat restoration needed to return monarchs
to a sustainable population size require the planting of 1.3–1.6 billion stems of milkweed in the Midwest (Pleasants 2017; Thogmartin et al. 2017a). Yet, this conservation approach assumes that monarchs are able to locate and utilize milkweed stems equally across all types of landscapes.

Monarchs are able to visually detect milkweed from several meters away (Garlick 2007) and detect milkweed and flowering plants through olfaction from up to several hundred meters away (Blackiston et al. 2011; Grant et al. 2018). In addition, adult summer breeding monarchs can fly 15 km daily (Zalucki et al. 2016) and it is likely that their flight patterns differ in habitat-rich versus habitat-poor landscapes (Zalucki and Kitiching 1982; Zalucki 1983). Since monarch perceptual range is limited, isolated patches of habitat (i.e., in landscapes with few additional grassland patches) may be harder to locate.

Site selection

By using standardized sampling protocols and intentionally selecting grassland sites to span a range of landscape contexts and patch sizes, we tested the independent effects of landscape and patch-level characteristics on monarch abundance. Sixty “protected” grassland sites (i.e., park reserves, wildlife refuges, etc.) in Wisconsin (WI), USA were selected for surveys: 31 in northern and 29 in southern WI (Fig. 1). Sites were chosen from a broader list of potential properties to which we could gain access and permission for sampling, and generated from several sources: the Wisconsin Department of Natural Resources, the U. S. Fish and Wildlife Service, and The Nature Conservancy. All sampling sites occurred in landscapes that contained additional grasslands. To ensure that sites spanned a range of local and landscape characteristics of interest, the properties were selected from a large pool of potential sites in this region to span a range of patch sizes (0.9–700 ha of contiguous grassland) and grassland context (1–45% grassland at 10 km buffer around each patch) and to ensure that these variables were uncorrelated ($r = 0.36$, Online Appendix A).

All sites were surveyed in both 2018 and 2019, with each site surveyed in three time periods (early: approximately June 1–June 22, middle: approximately June 23–July 14, and late: approximately July 15–August 9) over the course of each summer field season to account for phenological changes in vegetation and monarch presence in the Midwest (Oberhauser et al. 2017).

Landscape-level and area-based characteristics

We used the proportion of grassland in the surrounding landscape as a proxy for additional available monarch habitat, given that most grasslands have milkweeds and nectar plants (Thogmartin et al. 2017b). We used area-based landscape metrics, specifically the proportion of suitable habitat in the landscape within a given buffer, as they are reliable metrics of patch isolation when compared to simple distance-based or omni-directional distance-based metrics (Bender et al. 2003; Fahrig 2013). We used a digital raster-based land cover classification map with a grain size of 30 m $\times$ 30 m to determine, for a 10 km-radius circular buffer surrounding each survey site, the proportion of grassland habitat in this area (combining NLCD land cover classifications of grassland, pasture/hay, and/or herbaceous wetland, National Land Cover Dataset 2016, Dewitz 2019). We calculated landscape metrics using the landscapemetrics and tigris packages in R (R Core Team 2019; Hesselbarth et al. 2019; Walker 2020). Using the lsm_c_pland function, we evaluated the proportion of grassland within 10 km of each survey site. Because roadways can serve as corridors along which monarchs reach given habitat patches, we calculated road density (meters of road per km$^2$) within 10 km of a site to quantify additional potential habitat suitable for monarch recruitment in the landscape (United States Census Bureau 2019). We included forest edges, which represent potential monarch habitat and also barriers to monarch movement (Ries and Debinski 2001), as a variable by calculating forest edge density within 10 km of a site to using the lsm_c_ed function (Hesselbarth et al. 2019). To measure the size of each patch, we calculated the amount of contiguous grassland at a survey site using the lsm_p_area function (Hesselbarth et al. 2019).

Rather than initially testing landscape effects on monarchs at multiple buffer scales, we chose a priori the 10 km scale of analysis based on two factors. First, monarchs are strong fliers and females have an estimated daily travel maximum of 15 km and the 10 km scale was a conservative compromise on the area used by a foraging monarch over the course of a
sampling period (Zalucki et al. 2016). Second, multiple buffer methods have several statistical issues that complicate interpretation of results, including the higher likelihood of higher Type I errors (Miguet et al. 2016). Nevertheless, we also performed an additional set of post hoc analyses for each of the response variables with landscape characteristics measured at the 5 km and 20 km scales (see Online Appendices B–G). The results of these analyses support the same patterns and reach the same conclusions as the analysis at the 10 km scale, thus for simplicity we report here only the analysis at the 10 km landscape scale.

Patch quality characteristics

We measured several variables during each site visit: milkweed stem density (stems per m$^2$), milkweed species richness (number of unique species), and floral species richness (number of unique species in bloom) (See Table 1 and Online Appendix H). We used survey methods of the Integrated Monarch Monitoring Protocol (IMMP, Cariveau et al. 2019). In brief, this approach consists of setting up a rectangular sampling plot measuring 50 × 200 m and consisting of four transects which make up the 500 m perimeter of each plot. We randomly placed the survey plot in a grassland habitat within each site using the Create Random Points tool in ArcGIS (Esri 2018). To record floral species richness, all blooming plants within a meter of the transect lines were identified to species. We assessed milkweed density by placing a 0.5 m × 1 m quadrat on both sides of each transect line every 5 m along the 500 m perimeter, creating a 1 m$^2$ subplot at every 5 m mark (100 total subplots per survey plot). We recorded the number of milkweed stems rooted within the bounds of the quadrat, and estimated milkweed density as stems/m$^2$.

Fig. 1 Map of 60 sites within Wisconsin, USA surveyed for monarch butterflies in 2018 and 2019. Examples of sites with low and high grassland in the landscape within 10 km are shown at bottom left.
We excluded *A. verticillata* from milkweed and monarch metrics (except for Table 1) following Kasten et al. (2016) and Lukens et al. (2020). This exclusion was due to the large number of stems of this species found at some patches, which, if included, artificially inflated the stem density estimates because of *A. verticillata*’s small biomass compared to other *Asclepias* species. Some of our survey areas contained up to 4000 stems of *A. verticillata* (the next most common species, *A. syriaca*, had a maximum of 808 stems), making it difficult not only to compare to other species, but to count and search for monarch eggs and larvae (hereafter “immatures”) thoroughly and with the same effort. Half of our sites contained *A. verticillata*.

Monarch surveys

We used a modified Pollard walk to count monarch adults within 5 m of each transect (Pollard 1977; Cariveau et al. 2019). Surveys of monarch adults were conducted only when environmental conditions were optimal for butterfly activity: 0900–1600 h, temperature 18–33 °C, wind speeds < 39 km/h, and no precipitation. We conducted Pollard walks before the patch quality characterization so that the adult count was not influenced by vegetation surveyors.

Surveys of monarch immatures were conducted during a second perimeter walk of the plot, in conjunction with the survey of patch-quality characteristics (above). We walked along the perimeter of the survey plot and examined all milkweed stems within one meter of the transect lines. Each milkweed stem encountered was inspected for monarch immatures. In most cases, each milkweed stem encountered (117 ± 112 stems, mean ± SD) was inspected for monarch immatures, although we stopped inspecting after 200 stems at some high milkweed density sites to avoid observer fatigue.

We calculated immature monarch abundance per stem (immatures observed/stems inspected). This value provides a familiar metric for land managers interested in predicting the number of monarchs their habitat restoration could produce based on the number of stems that are feasible to plant, in accordance with national conservation goals expressed in the number of new milkweed stems needed to restore the monarch population (Thogmartin et al. 2017a). In addition, we calculated monarch immature density (immatures/m²) by multiplying immature abundance per stem (immatures/stem) by milkweed stem density (stems/m²). This metric provides an estimate of the abundance of immature monarchs on an area-based, patch-level spatial scale rather than a *per stem* metric.

Statistical analysis

We used multiple regression to assess the relationship between monarch abundance and the two general categories of variables of interest: landscape characteristics and local patch-level characteristics. Response variables were measured as the count of adult monarchs, monarch immatures per milkweed stem, and monarch immatures per m².

We created three separate mixed-effects regression models to assess whether landscape characteristics (surrounding proportion of grassland, forest edge density, road density) and local, patch-level characteristics (patch size, milkweed density, floral richness) predicted the response variables. We used nectar
flower richness in our analyses rather than flower abundance as these variables were highly correlated \((r = 0.88)\) and only one could be used in the statistical models, and also because at some sites highly abundant species were known not to be favored by monarchs for foraging and thus could skew the analysis. We included the interaction between the proportion of grassland in the landscape and patch size to examine whether patch size effects varied by landscape context. To facilitate comparison of covariate effects ranging over different scales, predictor variables were scaled using the \textit{scale} function in R (R Core Team 2019).

To account for additional temporal and spatial variation, other covariates in the full models included year (2018, 2019), survey period (early, middle, late) within the season, and a random effect of site nested within region (north or south Wisconsin) to account for repeated samples and different regions. We performed a Moran’s test using the \textit{Moran.I} function in the package \textit{ape} (Paradis and Schliep 2018). Predictor variables were uncorrelated in the full models (VIF < 3).

To address overdispersion issues in the model for monarch adults, we used the negative binomial family of distributions in the \textit{glmmTMB} package (Brooks et al. 2017) to model the data. The response data for the adult count model were zero-inflated; to account for this inflation we used a zero-inflation formula in models for milkweed density and floral richness. For the models predicting monarch egg and larva density, we used the Tweedie family of distributions (Shono 2008). The Tweedie family of distributions accommodates zero inflation, so there was no need for a separate zero-inflation component in these models. For model selection, we passed each full model through the \textit{dredge} function in the \textit{MuMIn} package (Barton 2019), reporting models with \(\Delta\text{AIC} < 2.1\) from the best-fit model as competing models (Akaike’s Information Criterion; Burnham and Anderson 2002). Model assumptions and fit were evaluated, in part, with the \textit{DHARMa} package (Hartig 2020). We calculated \(R^2\) values with the \textit{r2} function in the \textit{performance} package (Lüdecke et al. 2020).

### Results

#### Site characteristics

Our study sites varied in size from 0.9 to 700 ha of contiguous grassland \((93 \pm 138 \text{ ha}; \text{ mean} \pm \text{ SD})\), and the area within 10 km of them contained 1–45% grassland \((21 \pm 8\%; \text{ mean} \pm \text{ SD})\) (Online Appendix A). All sites contained at least some milkweed (Table 1), and we observed six different milkweed species overall \((\text{mean} = 1.83 \text{ species per site})\), with a mean milkweed density of 0.434 stems per m\(^2\). \textit{A. syriaca} was the most abundant, present at all but one of our study sites \((\text{mean} = 0.429 \text{ stems per m}^2)\). On average, there were 8.6 blooming plant species per site \((\text{range} = 0–24)\). We observed at least one adult monarch during 58% of our visits, and at least one immature monarch during 71% of our visits. There was no evidence of spatial autocorrelation between sites.

#### Adult monarch abundance

The full model with milkweed density and floral richness in the zero-inflation formula had the lowest AIC when compared with other combinations of variables. The best-fit model and all three competing models \((\Delta\text{AIC} < 2.1)\) predicting adult monarch abundance at a patch included the landscape-level variables of surrounding grassland and road density as well as local-scale variables of milkweed density, floral richness, and survey period (Table 2, Fig. 2). The amount of grassland in the surrounding 10 km had a negative association with adult abundance (Fig. 2A), as did road density (Fig. 2B). Within a patch, milkweed density and floral richness both had a positive relationship with monarch abundance (Fig. 2C, D); the effects of these predictors were of approximately equal magnitude (Table 2). In addition, we observed more adults during the second survey of the season than the earlier or later surveys. Other variables (forest edge density, patch size, year of survey, and the interaction effect between landscape grassland and patch size) were never or rarely present in the top models, and their coefficients were small when they were included. Interpretations of these models should be made with some caution based on the moderate amount of variation explained by the variables, which imply there are other factors that also influence
monarch patterns. Analyses of adult abundance at different spatial scales showed similar patterns (Online Appendices B, E).

Egg and larva density

Variability in monarch immatures per m² was most consistently explained by milkweed density (present in all 10 of competing best fit models) and year (Table 3, Fig. 3A). There were more immature monarchs per m² with higher milkweed densities, and more immature monarchs per m² in 2019 than in 2018. As with adult monarchs, immatures per m² were negatively associated with the amount of grassland in the surrounding landscape (present in 4 of 10 competing models, Fig. 3C), but road density had a small positive effect (present in 5 of 10 competing models, Fig. 3B). There tended to be more immatures per m² in the middle of the season (Table 3). Forest edge density, floral richness, and the interaction effect between surrounding grassland and patch size were not included in any of the best-fit models. Patch size had a small negative effect on immatures per stem in 4 of 10 competing models. Survey period and the interaction effect between surrounding grassland and patch size were not included in any of the top ten models. Analyses of egg and larva density at different spatial scales showed similar patterns to those at 10 km (Online Appendices C–F).

Discussion

In grassland patches occurring across two orthogonal landscape gradients of patch size and grassland in the
surrounding landscape, we found a negative association between the amount of potential monarch habitat in the surrounding landscape and adult monarch density in a patch and, to a lesser extent, egg and larva density. Interestingly, patch size did not affect monarch adult abundance along the transects, nor was there a significant effect of the interaction between patch size and the amount of habitat in the surrounding landscape. Furthermore, we found that higher milkweed density resulted in more monarch adults at patches, and was in turn associated with higher egg and larval density per unit area. These findings suggest that high-quality patches of habitat occurring in landscapes with relatively few other habitats supported the highest densities of immature and adult monarchs, irrespective of patch size.

Effects of landscape-level variability on monarchs

Our results have implications for considering how local monarch habitat can be established given the landscape context. That the adult monarch abundance at a patch was negatively associated with the amount of habitat (both grassland and roadsides) in the surrounding landscape measured at the 10 km scale suggests that landscapes in which habitat is limited can be valuable places for monarch habitat restoration. It is not clear from this study what mechanism may be...
influencing this pattern, though these results indicate that isolated, non-contiguous habitat patches could be functionally connected likely due to monarchs’ strong flying and navigational abilities as a migratory species (With 1997; Tischendorf and Fahrig 2000). A similar, albeit weaker pattern of lower egg and larval density in landscapes with less grassland habitat suggests that recruitment may be reflecting the adult patterns of abundance.

While some studies have found a positive correlation between the amount of preferred habitat in the surrounding landscape and insect abundance (Chaplin-Kramer et al. 2011), more recent syntheses suggest that the patterns may be more species and context dependent than previously observed (Bergman et al. 2018; Karp et al. 2018; Kleijn et al. 2018). Our findings suggest that in a landscape with less overall grassland available adult monarchs could become concentrated in the few grasslands that are available to them. Though the specific mechanism for the pattern needs to be tested, this pattern could suggest a greater rate of immigration and/or retention of monarch butterflies in grassland patches located in low grassland landscapes relative to high grassland landscapes. Different scales of landscape analysis yielded similar patterns.

Forest edge density on a landscape scale did not affect monarch abundance. This result could have been due to forest edges playing dual but opposing roles as both a barrier to monarch flight (Ries and Debinski 2001) and as habitat containing milkweed and blooming plants in the margins. It is also possible that we saw no effect from forest edge density because this metric is more influential on a smaller, more localized spatial scale than within our scales of analyses (< 5–10 km).

**Effects of patch size on monarchs**

While the resource concentration hypothesis posits that specialist herbivore insects are more likely to find and linger within larger habitat patches (Root 1973; Hill et al. 1996), we found that patch size did not predict adult monarch density. Previous researchers reported a positive effect of patch size on monarchs (Davis et al. 2007; Dinsmore et al. 2019). Patch size assessment differed between our study and theirs, which may account for different results. We measured the total area of contiguous grassland as the patch, whereas previous studies measured the total amount of grassland within a smaller area (~ 1 km) surrounding the spot at which monarch density was assessed. The relationship between patch size and butterfly density is likely to vary with species’ vagility and level of host plant specialization. The lack of response to local patch area is observed in other lepidopterans such as the diamondback moth (*Plutella xylostella*) and the great spangled-fritillary (*Speyeria cybele*) (Grez and

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**Table 3** The ten best-fit models (ΔAIC < 2) predicting monarch egg and larva densities per m² as a function of predictor variables

| Model | Road density | Surrounding grassland | Milkweed density a | Patch size | Survey period in summer | Year* | Δ AIC | R² |
|-------|--------------|-----------------------|--------------------|------------|-------------------------|-------|-------|-----|
| 1     | –            | –                     | 0.652              | –          | –                       | 2019 > 2018 | 0.00  | 0.359 |
| 2     | 0.156        | –                     | 0.662              | –          | –                       | 2019 > 2018 | 0.19  | 0.358 |
| 3     | –            | –                     | 0.673              | –          | Middle > late > early   | 2019 > 2018 | 0.37  | 0.399 |
| 4     | 0.156        | –                     | 0.683              | –          | Middle > late > early   | 2019 > 2018 | 0.55  | 0.398 |
| 5     | –            | – 0.144               | 0.655              | –          | –                       | 2019 > 2018 | 0.70  | 0.360 |
| 6     | 0.153        | – 0.140               | 0.665              | –          | –                       | 2019 > 2018 | 0.92  | 0.356 |
| 7     | –            | – 0.150               | 0.676              | –          | Middle > late > early   | 2019 > 2018 | 0.95  | 0.400 |
| 8     | 0.154        | – 0.146               | 0.687              | –          | Middle > late > early   | 2019 > 2018 | 1.15  | 0.398 |
| 9     | –            | –                     | 0.641              | 0.088      | –                       | 2019 > 2018 | 1.53  | 0.360 |
| 10    | 0.162        | –                     | 0.649              | 0.098      | –                       | 2019 > 2018 | 1.59  | 0.358 |

Values are the scaled parameter estimates for continuous variables, and order of levels for categorical variables (survey period, year). Dashes with no numbers (–) indicate that the covariate was excluded from a model. Significant predictor variables (p < 0.05) in the full model are denoted with an asterisk (*). Predictor variables that did not appear in any of the ten best-fit models (floral richness, forest edge density, and the interaction of patch size × surrounding grassland) are not listed.
González 1995; Davis et al. 2007) due in part to their ability to disperse widely, an ability shared by monarchs.

We found weak evidence that smaller patches had higher densities of monarch immatures. This finding aligns with the results of Grant et al. (2018) who suggested that small patches contribute to monarch recruitment, though this effect of patch size was attributed to an effect of connectivity. We found no support for an interaction between patch size and the amount of surrounding grassland again suggesting that as strong fliers, monarchs may easily pass over habitat boundaries and through inhospitable areas to access both small and large patches (Ries and Debinski 2001).

Fig. 3 Plots of relationships between monarch eggs and larvae per m² at a patch and the predictor variables that were among the best-fit models based on AIC (see Table 3). Solid lines indicate significant predictor variables. Dashed lines indicate nonsignificant predictor variables but were included in ≥ 4/10 of the best-fit models. The gray ribbon represents the 95% confidence interval. A shows the relationship between monarch egg and larva density per m² and milkweed density, which was included in all of the top ten models selected based on lowest AIC. B shows the relationship between egg and larva density per m² and road density in the landscape. C shows the relationship between egg and larva density and the amount of grassland in the surrounding area within 10 km of the patch. Model 6 (Table 3) was used to plot these relationships because it was the model with the lowest AIC that contained the three variables most commonly found in the top ten models.
Effects of patch quality

One of the strongest patterns we observed was the effect of local patch quality characteristics on the density of both immature and adult monarchs. Milkweed stem density within the patch had a consistent and significantly positive relationship on both immatures per m² and adult abundance, despite the fact that immatures and adults have different resource requirements. This finding suggests that an increased rate of gain of adult monarchs (or alternatively, longer stays within the patch) exceeds the potential resource dilution effect of females ovipositing across more available host plants. The resource dilution effect is seen with the negative relationship between milkweed density and immatures per stem (rather than per m²; Otway et al. 2005; Stephens and Myers 2012). This pattern (i.e., rate of gain exceeding dilution) could also occur if females visiting high-density milkweed patches experience increased fecundity because their

### Table 4

The ten best-fit models (ΔAIC < 2) predicting the relationship between eggs and larvae per stem at a patch and each of the predictor variables

| Model | Road density | Forest edge density | Surrounding grassland | Milkweed density* | Floral richness* | Patch size | Year* | Δ | AIC | R² |
|-------|--------------|---------------------|-----------------------|-------------------|-----------------|-----------|-------|---|-----|-----|
| 1     | –            | –                   | –                     | –                 | 0.333           | –         | 2019 > 2018 | 0.00 | 0.283 |
| 2     | 0.146        | –                   | –                     | –                 | 0.324           | –         | 2019 > 2018 | 0.16 | 0.267 |
| 3     | –            | –                   | – 0.159              | –                 | 0.332           | 0.310     | 2019 > 2018 | 0.18 | 0.283 |
| 4     | 0.141        | –                   | – 0.155              | –                 | 0.323           | –         | 2019 > 2018 | 0.40 | 0.266 |
| 5     | –            | – 0.120             | –                     | –                 | 0.330           | 0.315     | 2019 > 2018 | 1.02 | 0.276 |
| 6     | –            | –                   | –                     | –                 | 0.311           | 0.299     | 2019 > 2018 | 1.03 | 0.285 |
| 7     | 0.140        | –                   | –                     | –                 | 0.304           | 0.301     | 2019 > 2018 | 1.30 | 0.267 |
| 8     | –            | –                   | – 0.144              | –                 | 0.314           | 0.306     | 2019 > 2018 | 1.56 | 0.284 |
| 9     | 0.127        | – 0.087             | –                     | –                 | 0.323           | 0.313     | 2019 > 2018 | 1.72 | 0.263 |
| 10    | –            | – 0.128             | –                     | –                 | 0.306           | 0.312     | 2019 > 2018 | 1.87 | 0.277 |

Values are the scaled parameter estimates for continuous variables, and order of levels for categorical variables (survey period, year). Dashes with no numbers (–) indicate that the covariate was excluded from a model. Significant predictor variables (p < 0.05) in the full model are denoted with an asterisk (*). Predictor variables that did not appear in any of the ten best-fit models (survey period in summer and the interaction of patch size × surrounding grassland) are not listed

**Fig. 4** Relationships between monarch egg and larva per stem density at a patch and the predictor variables that were in the top selected model based on AIC. The gray ribbon represents the 95% confidence interval. Monarch egg and larva per stem density is (A), negatively associated with milkweed density; and B positively associated with floral richness in the patch.
searching time is decreased. While we did not measure oviposition rates by individual females, the fact that we saw more adults in patches with higher milkweed densities suggests that our finding of more immatures per unit area is at least partly due to more females or longer stays in the patch, and not just more eggs per female. The positive relationship we found between milkweed density and immatures per m² is in line with the resource concentration hypothesis which posits that denser stands of host plants will recruit more specialist herbivores than sparse stands (Hambäck and Englund 2005).

A study by Kasten et al. (2016) found that as milkweed density increased along the roadsides, egg density on milkweeds reached an asymptote. In our study, however, immature monarch density per unit area continued to increase with increasing milkweed density. The reasons for this difference are not immediately apparent, since egg and larva density leveled off at 0.6 milkweed stems per m² in the Kasten et al. (2016) study, while in our study immature density was still increasing at 5 milkweed stems per m². Our findings suggest that more adult monarchs are attracted to grassland patches with higher milkweed densities or that they stay longer once they get to a patch, and that this results in increased monarch recruitment, at least in the A. syriaca dominated grasslands we studied (Table 1).

An alternative way of expressing monarch abundance is on a per stem of milkweed basis, rather than on a per m² basis. The per stem approach to reporting immatures is often used in reporting associations between milkweeds and monarchs (e.g. Pleasants and Oberhauser 2013; Pleasants 2015; Stenoien et al. 2015, etc.) and can help land managers understand how many butterflies will result from planting a certain number of stems. We found that patches with lower milkweed densities had more eggs and larvae per stem. However, overall more eggs and larvae per m² were found in patches with higher milkweed densities, indicating a net effect of more milkweeds producing more monarchs. These results align with others who have surveyed monarch eggs and larvae on a per stem basis (Kasten et al. 2016). This effect is expected if the same number of eggs were spread out over a larger number of host plants—if eggs were being diluted over more host plants. However, the fact that we found both more adults and more immatures on a per area basis with increasing milkweed density documents the importance of assessing egg and larva density on a per area basis. This metric predicts population-level outcomes that scale with both habitat area and host plant density and thus provide a better understanding of how much habitat is needed to support a sustainable monarch population. The positive relationship between immatures per m² and milkweed density indicates that planting more milkweed stems should result in higher monarch recruitment at a patch.

Higher floral richness and abundance led to more adult monarchs. As monarch nectaring is important to fuel flight during the breeding season (Stenoien et al. 2018; Lukens et al. 2020), the greater the variety of nectaring plants, the more likely that plants with high rewards will be encountered. In our models, we used floral species richness; floral richness and abundance were correlated and therefore higher floral abundance will also likely lead to more adult monarchs. Previous research suggests that butterfly dispersal is tied to nectar resources (Potts et al. 2009), and our finding that adult abundance increases with floral richness supports previous findings. Yet, the lack of an effect of floral richness on immature density suggests that milkweed in areas with poor floral richness may nevertheless support monarch recruitment despite offering a smaller nectar reward for adults. The lack of correlation between immature monarch density and floral richness may imply that females still oviposited at patches with lower nectar diversity, but possibly left more quickly in search of nectar resources.

Conclusion

Planning and managing butterfly habitat conservation and restoration can be improved by understanding how use of a site is affected by landscape- and patch-scale characteristics (Matter and Roland 2002). Monarchs must be able to find and use habitat patches during their breeding season if the population is to reach sustainable levels. If conservation efforts are not informed by an understanding of the effects of landscape components on monarch patch use, restorations may take place at scales or in landscapes that do not result in the greatest benefits to the population. Similarly, in order to avoid creating suboptimal habitat for monarchs, restoration managers should consider how milkweed density and flowering species...
richness and abundance contribute to monarch recruitment.

We found more adult monarchs in landscapes with less grassland and therefore more isolated patches, reflecting the value of creating, improving, and expanding patches in landscapes where little habitat exists. Our findings on the impacts of patch quality reinforce the importance of plentiful milkweed stems; higher stem densities resulted in higher densities of eggs and larvae per m². While the existing milkweed densities in our study sites did not identify a point of diminishing returns with respect to milkweed density, previous research (Kasten et al. 2016) suggests that this saturation point may exist.

Land managers must also decide how many additional flowering species to include in restorations focused on monarch conservation based on cost and other considerations. We found more adult monarchs in sites with more flowering species. However, our finding that blooming plant diversity did not affect egg and larva density suggests that females lay just as many eggs in less florally diverse patches and that our observation of more adults might be due to females staying in more diverse patches longer to nectar without laying more eggs.

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Declarations

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