The distribution, seasonality, and future conservation of tiger beetle (Coleoptera: Cicindelidae) species in Indiana, USA

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Introduction

Tiger beetles (family Cicindelidae or subfamily Cicindelinae) are insects that are widespread throughout the world. Currently, there are 2,971 species and 924 subspecies (Anichtchenko 2024), and new taxa are described each year. Currently, there are 131 species and 181 subspecies recorded from the U.S (Anichtchenko 2024). Adult tiger beetles are usually found in open, dynamic habitats, like sand dunes, salt flats, playas, river edges, ocean beaches, grasslands, agricultural fields, and disturbed areas (Knisley 2011). Adults are active diurnal predators that inhabit open sunlit habitat patches in order to maintain high body temperature for capturing prey. Many tiger beetles are generalist predators, which will prey on many small invertebrates. Larval tiger beetles are burrow-dwelling sit-and-wait predators, and they are usually found in similar habitats as adults. Generally larvae are absent from densely vegetated habitats (Knisley and Schultz, 1997).

Tiger beetles are considered indicator species for certain ecosystems as they are often habitat specialists and their global distribution, sensitivity to habitat changes, and conspicuous adults (Pearson and Cassola 1992). Broadly, tiger beetles can be classified into three habitat preference categories: beach species, riparian species, and barren/savanna species (Schlesinger and Novak 2011). Much evidence shows that each category can be a good indicator to the corresponding habitat type. For beach habitat, Costa and Zalmon (2019) suggest that *Cylindera nivea* Kirby shows a high sensitivity score to human impacts and urbanization in Brazillian coast, which can destruct suitable beach habitats of the species. For barren habitat, Knisley and Arnold (2004) suggest that *Cicindela ohlone* Freitag, Kavanaugh and Morgan was restricted to cattle trails due to vegetation encroachment of inland habitats. Some human activities are especially destructive to tiger beetles, like river dam construction and channelization, which is responsible for many tiger beetles extirpation. The establishment of Shasta and Oroville Dams in California caused extinction of *Cicindela hirticollis abrupta* Casey due to the loss of point-bar habitats (Knisley and Fenster, 2005). The extirpation of federal critically endangered species *Ellipsoptera puritana* G. Horn along the Connecticut River is also due to construction of 17 dams (Vogler et al. 1993).

In addition to general habitats, some tiger beetle species also have a narrow range of microhabitat tolerance, especially of soil conditions. This was first suggested by Shelford (1907), and Dunn (1978) later concluded that this might be due to the temperature and moisture

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requirements of the larva. The protected species *C. patruela* Dejean (listed by NatureServe) only inhabits open forests and savannas with dry and coarse-grained sandy soils (Knisley and Schultz 1997). Schincariol and Freitag (1991) suggest that species in *Cicindela splendia* group show a strong association with clay soil, particularly Chenozem and Luvisols. A study conducted by Cornelisse and Hafernik (2009) points out that soil moisture and texture are important factors for female oviposition of *C. hirticollis*, while soil PH and salinity is more important for *C. oregona*. Therefore, many species show strong specialization to particular microhabitats due to their life cycle and larva biology, while soil temperature, moisture, PH, and bio-activity might be important factors.

Because of splendid appearances of many species, tiger beetles are collected and observed by many amateur entomologists, providing comparatively more data on species abundance and distribution than other Coleoptera. The popularity of tiger beetles is also because of to the comparatively stable taxonomy of tiger beetles and the ease of identifying many species due to numerous accessible field guides (eg. Pearson et al. 2015; Brust 2020) and community science websites (eg. BugGuide, iNaturalist). Currently, there are 125,307 observations (mostly living adults) of tiger beetles on iNaturalist, a platform providing valuable citizen science data on biodiversity (Cecco et al 2021), with 113,610 of them being "research grade", meaning that the observation has been identified to species and confirmed by at least two users, and the data has been included in GBIF (Global Biodiversity Information Facility). Amateurs efforts are also important for the conservation of tiger beetle species, as individual petitions play an important role in considering a species for listing, such as *Cicindela ohlone* and *Cicindela albissima* Rumpp (Knisley et al 2014).

Tiger beetles in the U.S midwest have generally been well-studied. Graves and Brzoska wrote a book about tiger beetles of Ohio (1991), including taxonomy, distribution, and ecology of 21 tiger beetle species recorded from Ohio. Among them, 18 species also have confirmed records in Indiana besides species with doubtful records (*C. spendida, C. limbalis, and C. ancocisconensis*). Garner (1980) has reported 21 species of tiger beetle in Illinois, but one species (*Parvindela celeripes*) is in error or based on strays (Bousquet 2012). Excluding two species with doubtful distribution (*C. spendida, C. limbalis*), 17 species also occur in Indiana. Graves also systematically studied tiger beetle species in Michigan (1963), reported the occurrence of 14 species, and 13 of them are shared with Indiana. A recent book about tiger beetles in Minnesota, Wisconsin, and Michigan by Brust (2020) includes 21 species. Although tiger beetles in Kentucky have not been systematically studied, Bousquet's catalog (2012) includes 21 species, and 17 species are shared with Indiana besides doubtful species. In general, many tiger beetle species are widespread in the Midwest, except species generally distributed in the south (like *Tetracha Carolina*) or species associated with specific habitats (eg. *C. ancocisconensis, C. marginipennis*).

The first key to tiger beetles of Indiana was published by Blatchley (1910) in his *An illustrated descriptive catalogue of the coleoptera or beetles (exclusive of the Rhynchophora) known to occur in Indiana : with bibliography and descriptions of new species*. Sixteen species were reported by Blatchley (1910) with a brief discussion of distribution and habitats. Goldsmith published a study of Indiana tiger beetles (1916), and made observations in 21 counties of the state. All observation localities were presented on a map attached at the end of the article. A total of eight tiger beetle species were recorded, and their habitats and behaviors were discussed in detail. After that, Montgomery and Montgomery (1930) reported 17 species in Indiana, with *C. celeripes* (later verified as *Parvindela cursitans*) newly added to the list. Knisley then published a study of tiger beetles from Indiana Dunes region (1978), with 8 species were recorded, and their specific biology was discussed, including habitat preferences, abundance, density, seasonality, and spatial and temporal segregation. Later the author later published a synopsis of tiger beetles in Indiana (1987) which includes 20 species. *Cicindela marginipennis* was added and the potential occurrences of *C. limbalis* and *C. splendida* was suggested. Distribution of all known species were presented in several maps, and a key of all species was included. Most recently, Bousquet's *Catalogue of Geadephaga of North America* (2012), includes state-level distribution of all tiger beetles from North America and reported 21 species in Indiana**.**

Indiana, a midwestern state with extensive agricultural activities, has undergone significant landscape changes in the past century, including habitats of all known tiger beetle species.

According to Whitaker et al (2012), there were 3,838,042 acres of timber land in 1901, and increased to 4,343,879 in 1992. Forest coverage has increased by 52,500 acres since 1998 and 450,000 acres since 1950. However, original forest continued to decline since 1900, the same as many forest-dwelled species. Prairie has undergone significant destruction since the 20th century. Gordon (1936) shows that there were about 2,155,876 acres of prairie in Indiana, while Lindsey et al. in 1965 indicates 601,664 acres of dry prairie in the state. In 2000, The Nature Conservancy estimated that only about 1,000 acres of original prairie remained, and restored 5,400 acres after that (U.S Department of Agriculture 2022). Although the restoration program since the 1980s has recovered some natural prairie habitats, its current coverage is still far less than the original proportion. Native species in prairie habitats were considerably reduced since 1900, and many were extirpated in 2000 (Whitaker et al. 2012). Although rarely studied, many barren lands have disappeared in the 20th century. Floods caused by large dams destroyed sand bars and gravel bars. Aquatic ecosystem has also been affected dramatically, including riparian vegetation removal, stream channelization, draining of wetlands, and daming of multiple rivers (Whitaker et al. 2012).

As many species are habitat specialists, tiger beetles in IN are expected to undergo potentially distribution changes due changes of suitable habitats as the result of human modifications and the widespread impacts of global climate change, which is expected to become more significant according to most climatic models. The second type of impact has been observed in Carabidae (Qiu et al 2023), suggesting that different Carabidae species (including tiger beetles) respond differently to climate change in both abundance and distribution ranges. A particular concern noted for three species with conservation concerns: *Ellipsoptera lepida* (Dejean, 1831) and *C. patruela* are currently listed as vulnerable by NatureServe (2024). while *C. marginipennis* is currently listed as critically imperiled in Indiana. Besides, other rare species may also undergo significant habitat shrinkage or even be extirpated throughout the state.

This study aims to 1) compile a checklist of all species known from Indiana based on the most recently-collected specimens or observations ; 2) evaluate records of several species that have doubtful distribution in Indiana 3) assess the current distribution of species within the state and predict their future distribution; 4) provide insights into the future conservation of tiger beetles from Indiana.

Based on findings of previous studies (eg. Dangalle et al. 2011) and the combination of the significant habitat alterations and global climate change in the past century, we hypothesize that tiger beetle species in Indiana will exhibit changes (both expansion and contractionbased on habitat specialization) in their distribution.

Materials and Methods

Preliminary species occurrence data

Specimens from the following institutional collections were examined: Purdue Entomological Research Collections (PERC), Depauw University, and The Field Museum of Natural History (FMNH). Other occurrence records of tiger beetles were derived from GBIF (2024) and Inaturalist. Doubtful species records were all checked by contacting curators for specific information.

For each species, county-level distributions expand upon Knisley's map (1987), with additional information on newly recorded localities and other pertinent comments. Newly recorded localities are marked with an asterisk.

To illustrate the full distribution of each species within the state, county-level distribution maps for each species were generated by QGIS. Counties with confirmed distribution record only from Knisley (1987) are highlighted with right hashed black slashes, while newly recorded county records

are marked with left hashed red slashes. For species of particular conservation concern, counties with historical occurrence sites but no current records of the species are outlined in red (*C. marginipennis*, fig. 6) . Finally, counties without any tiger beetle records are filled with red color.

The seasonality of all species in Indiana is presented in seven seasonality charts, with two or three species per chart. These charts were generated in Excel.

Results

Catalog and Seasonality of Tiger Beetle Species in Indiana

The combined data includes 2,122 records of 19 tiger beetle species in Indiana. A complete catalog is provided below. Newly recorded counties are marked with an asterisk.

***Apterodela (Protoapterodela) unipunctata* (Fabricius, 1775) (Fig. 1)**

Known Indiana distribution: Tippecanoe, Warren, Vermillion, Vigo, Putnam, Morgan, Owen, Monroe, Brown, Lawrence, Clark, Gibson, Posey, Vanderburgh, Perry, Crawford, Clark, Harrison*.
Remarks: This easily-recognized species was reported from central and southern Indiana. While recent records show its presence in the south, only a few old records are from central Indiana (Tippecanoe, Putnam). The species inhabits woodland, especially shaded forests (Pearson et al. 2015), which is abundant in many parts of the state. Therefore, the absence of its occurrence in forested areas of central Indiana might be due to sampling bias, as shaded woodland is not a suitable habitat for most tiger beetle species in Indiana. The species occurs from March to October, and reaches the peak in June (see Chart. 1). For further details see Discussion, below.

***Cicindela (Cicindela) duodecimguttata* Dejean, 1825 (Fig. 2)**

Known Indiana distribution: Lake, LaPorte, Lagrange, Starke, Pulaski, Fulton, Cass, Tippecanoe, Wayne, Vermillion, Vigo, Johonson, Owen, Brown, Franklin, Jackson, Knox, Gibson, Posey, Vanderburgh, Clark, Jefferson, Marion*, Fountain*, Harrison*.

Remarks: The species is widespread throughout the state. It often inhabits moist and sandy soils near water (Pearson et al. 2015). The species is easily confused with *C. repanda* (Stephen 2004), a commonly recorded species, and we hypothesize the low number of records of *C. duodecimguttata* may be due to misidentifications. The species occurs from March to October. The first peak is in April, and the second peak is in August (see Chart. 2).

***Cicindela (Cicindela) formosa* Say, 1817 (Fig. 3)**

Known Indiana distribution: Lake, Porter, LaPorte, Elkhart, Lagrange, Kosciusko, Newton, Jasper, Pulaski, White, Cass, Wayne, Vigo, Knox, Daviess, Martin, Jackson, Gibson, Perry, Posey, Tippecanoe, Sullivan*, Monroe*, Morgan*, Crawford*.
Remarks: This large species can be found in many places in the northern and southern part of the state. The species inhabits upland sandy areas with sparse vegetation but without standing water sources (Pearson et al. 2015). In Indiana, many observations and collected specimens are from northern part, probably because there are more abundant sandy areas (eg. Kankakee Sands,

Indiana Dunes National Park). The species always inhabit the same habitats as *C. scutellaris*, and their distribution nearly overlapped in Indiana. The species occurs from April to November, and reaches the peak in June (see Chart. 3).

***Cicindela (Cicindela) hirticollis* Say, 1817 (Fig. 4)**

Known Indiana distribution: Lake, Starke, Wayne*, Newton*, Porter*, Morgan*, LaPorte, Monroe, Jackson, Knox, Daviess, Clark, Posey, Vigo.
Remarks: Historical records show that the species was widespread throughout the state, but more recent records are restricted to the northern part of the state, near Lake Michigan. The species can be found in sandy edges near water, where *C. repanda* also presents. The species occurs from April to October, and reaches the peak in July (see Chart. 4).

***Cicindela (Cicindelidia) marginipennis* Dejean, 1831 (Fig. 5)**

Known Indiana distribution: Dearborn, Franklin, Wayne
Remarks: This threatened species is perhaps the most rarely collected species, and its distribution in Indiana is only restricted to several counties in the southeastern part, near the border of Ohio (Kritsky et al 2009). The species is absent in many historical sites due to habitat destruction, and its current distribution in Indiana only includes one locality in Franklin county (Kritsky et al 2009). For further details see Discussion, below.

***Cicindela (Cicindela) patruela* Dejean, 1825 (Fig. 6)**

Known Indiana distribution: Lake, Porter, Starke, Tippecanoe, Owen, Monroe, Brown, Lawrence, Morgan*.
Remarks: This rarely observed species was recorded in a few counties in northern and central Indiana, but there's no recent record of it throughout the state. The species prefers dry sandy soils in open mixed forests and often associated dry slopes with lichen and mosses (Pearson et al. 2015). Like its overall distribution, the distribution in Indiana may also be fragmented and localized. On the other hand, the species is similar to *C. sexguttata*, so some specimens of *C. patruela* might be misidentified as *C. sexguttata*, and its real distribution in Indiana might be larger. The species occurs from June to October, and reaches the peak in July (see Chart. 5). For details, see the discussion below.

***Cicindela (Cicindelidia) punctulata* Olivier, 1790 (Fig. 7)**

Known Indiana distribution: Lake, Porter, LaPorte, Lagrange, Steuben, Noble, Kosciusko, Pulaski, Newton, White, Benton, Tippecanoe, Boone, Marion, Vermillion, Fountain, Parkes, Posey, Putnam, Fayette, Shelby, Johnson, Morgan, Vigo, Owen, Orange, Monroe, Greene, Brown, Bartholomew, Jennings, Jackson, Lawrence, Daviese, Knox, Gibson, Dubois, Crawford, Harrison, Clark, Scott, Allen*, Clinton*, Elkhart*, Floyd*, Grant*, Hendricks*, Henry*, Hamilton*, Hancock*, St. Joseph*, Jasper*, Perry*, Randolph*, Switzerland*, Starke*, Wabash*, Warren*, Wells*, Maddison*, Sullivan*, Miami*, Marshall*.
Remarks: The species is commonly reported throughout the states. It is the second frequently encountered tiger beetle in Indiana. The species can be found in various open habitats, like agricultural fields, pastures, gardens, and dusty roads (Pearson et al. 2015). Knisley (1987) didn't find its occurrence in some eastern county, but recent updated data verified its presence. The species occurs from May to November, and reaches the peak in July (see Chart. 6).

***Cicindela (Cicindela) purpurea* Olivier, 1790 (Fig. 8)**

Known Indiana distribution: Jay, Putnam, Johnson, Clay, Vigo, Franklin, Monroe, Brown, Knox, Martin, Scott, Clark, Floyd, Crawford, Perry, Dubois, Pike, Posey, Parke*
Remarks: This species has been recorded from multiple counties in the southern part of the state. However, it is rarely collected, and no recent record is found. The species can be found in various open habitats, like grasslands, open fields, and forest clearings (Pearson et al. 2015). Some habitats may still remain intact in southern Indiana. The species occurs from February to October. The first peak is in May, and the second peak is in September (see Chart. 2).

***Cicindela (Cicindela) repanda* Dejean, 1825 (Fig. 9)**

Known Indiana distribution: Lake, Porter, LaPorte, Elkhart, Lagrange, Noble, Kosciusko, Starke, Jasper, Newton, Pulaski, Cass, Allen, Wells, Adams, Tippecanoe, Parke, Putnam, Knox, Morgan, Jackson, Monroe, Brown, Union, Franklin, Owen, Vigo, Greene, Lawrence, Johnson, Martin, Pike, Gibson, Orange, Scott, Posey, Vanderburgh, Crawford, Harrison, Clark, Jefferson, Dearborn, Spencer*, Warren*, Montgomery*, Fountain*.
Remarks: This common species can be found throughout the state. The species can be found in many open habitats, but commonly seen in sandy river banks (Pearson et al. 2015). There is no record of the species in some central and eastern counties, but we hypothesize that it is due to collecting bias in those areas. The survey conducted by Schnepp et al (2021) shows the presence of it in Shades State Park, which covers Montgomery, Parke, and Fountain county. Considering habitat similarity within the range, all three counties are listed here. The species occurs from February to December. The first peak is in June, and the second peak is in September (see Chart. 4).

***Cicindela (Cicindelidia) rufiventris* (Dejean, 1825) (Fig. 10)**

Known Indiana distribution: Tippecanoe, Wayne, Parke, Putnam, Vigo, Clay, Owen, Jackson, Union, Franklin, Decatur, Bartholomew, Brown, Monroe, Lawrence, Jennings, Johnson, Dearborn, Ohio, Jefferson, Scott, Gibson, Crawford, Harrison, Clark, Marion*, Hendricks*, Montgomery*, Fountain*.
Remarks: The species can be found in many central and southern counties of the state. It inhabits dry upland areas or sparsely vegetated clearings in open forest (Pearson et al. 2015). The species is not commonly collected in Indiana, and sometimes is confused with *C. punctulata*. The survey conducted by Schnepp et al (2021) shows the presence of it in Shades State Park, which covers Montgomery, Parke, and Fountain county. Considering habitat similarity within the range, all three counties are listed here. The species occurs from May to October, and reaches the peak in July (see Chart. 5).

***Cicindela (Cicindela) scutellaris* Say, 1823 (Fig. 11)**

Known Indiana distribution: Lake, Porter, LaPorte, Lagrange, Kosciusko, Starke, Jasper, Newton, Pulaski, White, Tippecanoe, Marion, Parke, Vigo, Sullivian, Knox, Daviese, Martin, Jackson, Gibson, Posey, Posey, Putnam*, Clark*, Morgan*.
Remarks: The species is widespread in Indiana. Previous records are mainly concentrated in the northern part, while updated data includes more records from the southern part of the state. The species inhabits dry sandy habitats, and can often be found together with *C. formosa* (Pearson et al. 2015). In pearson (2015)'s book, the author claimed that the species is absent in lower Mississippian River floodplain, which includes the entire southern and southeastern Indiana. The

new updated records have shown their potential distribution in those areas. The species occurs from February to November. The first peak is in May, and the second peak is in August (see Chart. 3).

***Cicindela (Cicindela) sexguttata* Fabricius, 1775 (Fig. 12)**

Known Indiana distribution: Lake, Porter, LaPorte, Lagrange, Noble, Kosciusko, Pulaski, Allen, Wells, Tippecanoe, Warren, Parke, Putnam, Morgan, Jackson, Monroe, Marion, Brown, Union, Franklin, Owen, Vigo, Greene, Lawrence, Johnson, Dubois, Pike, Huntington, Gibson, Orange, Scott, Posey, Vanderburgh, Crawford, Clark, Steuben, Fountain, Hamilton, Wayne, Vemillion, Clay, Perry, Spencer, Adams*, Delaware*, DeKalb*, Dearborn*, Bartholomew*, Benton*, Boone*, Cass*, Carroll*, Clinton*, Elkhart,*, Floyd*, Fayette*, Grant*, Hancock*, Harrison*, Hendricks*, Henry*, Howard*, Jennings*, Jefferson*, Maddison*, Miami*, Montgomery*, St.joseph*, Knox*, Newton*, Ohio*, Randolph*, Ripley*, Shelby*, Starke*, Switzerland*, Wabash*, Warrick*, White*, Whitely*, Marshall*, Union*, Tipton*
Remarks: This species has the most records in Indiana. It can be found in most counties, and the collection is abundant. The species usually inhabits open woodland and is most active in spring (Pearson 2015). The species may be confused with *C. patruela*, and they tend to share similar habitats. The species occurs from March to November, and reaches the peak in May (see Chart. 6).

***Cicindela (Cicindela) tranquebarica* Herbst, 1806 (Fig. 13)**
Known Indiana distribution: Lake, Steuben, Marshall, Starke, Cass, Tippecanoe, Putnam, Vigo, Owen, Lawrence, Bartholomew, Dearborn, Jackson, Martin, Monroe, Daviese, Knox, Pike, Gibson, Posey, Spencer, Perry, Crawford, Floyd, Orange, Dubois, Marion, Harrison*
Remarks: The species is widespread throughout the state, but most records are from the southern part. The species can be found in various open habitats (Pearson et al. 2015). The species occurs from March to November. The first peak is in May, and the second peak is in August (see Chart. 5).

***Cicindela (Cicindelidia) trifasciata** (Fabricius, 1781) (Fig. 14)**

Known Indiana distribution: Clark*, Porter*

Remarks: This species contributes to a new state record. One specimen was collected in Indiana Dune State Park in 1968, the northernmost part of the state. The most recent record is in Clark county, which is the southernmost part of the state. The species typically inhabits coastal areas. Considering the species has a strong dispersal ability and its widespread distribution in the New World (Pearson et al. 2015), it is not surprising that a few individuals will arrive in Indiana, but the establishment of local population has not been reported yet.

***Ellipsoptera cuprascens* (Leconte, 1852) (Fig. 15)**

Known Indiana distribution: Tippecanoe, Putnam, Vigo, Monroe, Daviese, Jefferson, Gibson, Posey, Warrick, Clark*
Remarks: The species was reported in several central and southern counties of the state. However, most recent records only show its presence in the southernmost part of the state. It is noteworthy that the species can be confused with *E. macra*. Some specimens collected from Northern Indiana are all misidentified *E. macra*. This species inhabits sandy beaches and mud flats near rivers and streams (Pearson et al. 2015). While suitable habitats seem to be abundant in many counties, the species is rarely reported, and many observations are from the same locality. The record of the species in Tippecanoe county needs further confirmation. The species occurs from May to

September, and reaches the peak in August (see Chart. 7).

***Ellipsoptera lepida* (Dejean, 1831) (Fig. 16)**

Known Indiana distribution: Lake, Porter, St. Joseph, Newton, Tippecanoe, Vigo, Sullivian, Daviese, Posey, Monroe*, Dearborn*
Remarks: The species used to be widespread throughout the state, but most recent records are all restricted to the northern part, near Lake Michigan. This species requires deep sand habitats, like inland dunes, sandy washes, and sandy ridges (Pearson et al, 2015). While Indiana had undergone significant landscape changes in the last century, many historical suitable habitats might be extirpated. Sandy areas near Lake Michigan are important refugees for this vulnerable species. For details, refer to the discussion below. The species occurs from May to September (except an occasional record in February), and reaches the peak in July (see Chart. 7). For further details see Discussion, below.

***Ellipsoptera macra* (Leconte, 1857) (Fig. 17)**

Known Indiana distribution: Lake, LaPorte, Porter, Tippecanoe*, Putnam*, Noble*, Kosciusko*
Remarks: The species was mainly recorded from northern part of the state, near Lake Michigan, but historical records indicate that its distribution can extend to South-central part of the state. It is noteworthy that the species can be confused with *E. cuprascens*, which is distributed in Sourthern part of the state, so records from south and central Indiana might be misidentification of *E. cuprascens*. Both species are recorded from Tippecanoe and Putnam county. We have verified specimens of *E. macra* in Tippecanoe county, but we cannot confirm *E. cuprascens* in Tippecanoe yet. For county-level distribution of two species, see Fig. 20. This species occurs in various open habitats, like mud and sand beaches of rivers and lakes (Pearson et al, 2015). The species occurs from May to September, and reaches the peak in July (see Chart. 7).

***Parvindela cursitans* (LeConte, 1857) (Fig. 18)**

Known Indiana distribution: Posey, Vanderburgh*
Remarks: This rarely observed species is only collected from the southernmost part of the state, and the most recent confirmed record is in Evansville, on the border of Indiana and Kentucky. It is also expected to be found in other nearby counties. For further details see Discussion, below.

***Tetracha virginica* (Linne, 1766) (Fig. 19)**

Known Indiana distribution: Tippecanone, Wayne, Morgan, Vigo, Monroe, Knox, Giibson, Posey, Clark, Lawrence, Crawford, Johnson, Bartholomew, Vanderburgh, Switzerland*, Fountain*, Putnam*, Parke*, Perry*
Remarks: This highly-distinguished species is widely distributed in the central and southern part of the state. It is often found in open grassy areas (Pearson et al. 2015). Generally, the species is not commonly observed in Indiana, which might be due to the nocturnal activity. The species occurs from May to November, and reaches the peak in July (see Chart. 1).

Discussion

Species composition and comparison with other midwest states

Overall, we confirmed specimens or observations of 19 tiger beetle species in Indiana. As expected, many species have wide distributions, and are also found in nearby midwestern states. The species composition of Indiana is most similar to Ohio (18 shared, 21 total) and Illinois (17 shared, 21 total). Michigan has fewer species than Indiana, but most of them are also shared (13 shared, 14 total). Kentucky has different ecoregions in the eastern and southern parts (eg. Southwestern and Central Appalachians), but tiger beetle species composition is still similar to Indiana (17 shared, 21 total), except C*. ancocisconensis* and *T. carolina.* Habitat-specific species have narrow distribution in the Midwest, like *C. marginipennis*, which is only known from Indiana, Ohio, and Kentucky, although the population in Kentucky is remote from those in Indiana and Ohio. Species generally found in the south also have peripheral distribution in southern midwest states, like Illinois and Kentucky, while the species may also present in extreme south of Indiana. *T. carolina* is actually counted as a species distributed in Indiana according to NatureServe, although no confirmed record can be found. The northern species *C. longilabris* is only found in the Upper Peninsula of Michigan, which has a different ecoregion than other southern Midwestern states.

Within the state, *C. punctulata* and *C. sexguttata* have the most records and widest distribution. The two species occupy different habitats, but both have been found in most counties (91% for *C. sexguttata* and 72% for *C. punctulata*). Although two species should have similar abundance, *C. sexguttata* has much more records than *C. punctulata*. This may be because of the bright green color of the species, which is more likely to attract attention. *Cicindea. punctulata* has a brown or black color that is similar to soil background, so it is not easy to find the species in some cases. Although woodland is not a common spot for tiger beetle collection, it is highly visible even to non-specialists. *Cicindela repanda* is also a commonly recorded species, but its habitat is always associated with water bodies, so the suitable habitats should be less than the previous two species. *Cicindela formosa* is also recorded frequently. It can be found in northern and southern counties, but is more common in northern counties, probably due to more intact habitats along Lake Michigan.

The occurrence of *Cicindela trifasciata* in Indiana.

This newly recorded species is only found in Porter and Clark county, on opposite borders of the state. Pearson et al (2015) states that the species can be far inland, including southern Illinois and Indiana, so the record in Clark county is likely to be an accidentally dispersed individual. Besides, an observation from Kentucky is just at the boundary of Vanderburgh county, suggesting its potential distribution in the entire southern boundary of the state. Graves (1981) reported that the species was found in oil rigs 160 km from mainland in the Gulf of Mexico, and Ralph and Brain (2000) reported the presence of the species in north-central Kansas, suggesting the strong dispersal ability of the species. Ralph and Brain suggested that the species may disperse along large rivers, which may explain its occurrences in Midwestern states. The occurrence in southern Illinois (also a new state record based on iNaturalist observation) is near the Mississippi river, and the occurrences in southern Indiana and northern Kentucky is along the Ohio River. On the other hand, the specimen found in Indiana Dunes State Park is likely a vagrant. The specimen was collected on

July 5, 1968, just in the interval of 1968 Atlantic hurricane season. The hurricane season began on June 1 and ended on October 21, and Tropical Storm Candy covered almost the entire eastern U.S, reaching as north as northern Indiana. National Weather Services indicates that the storm reaches Indiana on June 25, about ten days earlier than the collecting date. Therefore, the specimen from Porter county was likely blown north by the tropical storm. Despite the two records, no established population has yet been reported, suggesting a lack of suitable habitat in Indiana. Generally the species is found near salt-water sources, which are absent in Indiana.

Implication of species with conservation concern & rare species

Our result provides new insights into distribution trends for five species with conservation concerns. We here follow the ranking given by NatureServe for species that have overall conservation status other than Secure (G5). Among them, *C. marginipennis* is the most endangered species. NatureServe evaluates it as "vulnerable (G3)" in general and "critically imperiled" (S1) in Indiana. The latest study by Kritsky et al (2009) implies that the species can only be found in one site in Franklin county, while it is absent in two other historical sites (see figure. 6). Gwiazdowski et al (2020) suggests that the larvae can be easily found by looking for "throw piles", so future systematic surveys should try this method in potential suitable habitats. Considering the high habitat specificity of the species, the only reported site should be preserved immediately. Captive rearing and reintroduction is also a solution to recover the population, as Gwiazdowski et al (2020) shows the details of rearing the larvae. However, it should be implemented only if other suitable habitats are found. The article also mentioned the species's population structure in regional scales, but doesn't include populations from Indiana (see supplementary table). Future investigation may conduct population analysis and compare to other populations in the Midwest.

The other species with high conservation concern is *C. patruela*, which is in vulnerable status (S3, G3). The species was collected in several scattered counties (see figure. 6), and no recent records were found. Our material only includes four records, and the latest one is in 1965. The species has fragmented and localized distribution throughout the range are currently facing many threats (NatureServe). Agricultural conversion, logging, and fire suppression are main factors of habitat loss of the species (Environment Canada 2016). Combined with landscape changes in Indiana, we hypothesize that the species population might be very low in the state. Future efforts should survey more extensively in potential suitable areas, which have open forests with sandy soils. Also, habitat management is needed to keep them from vegetation encroachment. As the species may be misidentified as *C. sexgutatta*, future investigations can also check the collection of *C. sexgutatta* from institutions to see if there are new locality records of the species.

Ellipsoptera lepida also has vulnerable status (S3, G3) in Indiana. The species only inhabits deep sandy areas, and much evidence shows that it is absent from many historical sites due to sand excavation, development, and stabilization of sand dunes by lack of natural disturbance and encroaching vegetation (Pearson et al. 2015; Smith et al. 2021). Historical records show its distribution in scattered counties (see figure. 16) , but latest records only show its occurrence in the northern part, near Lake Michigan and Kankakee Sands. Considering landscape changes in the last century, the species might be extirpated from many historical sites due to habitat loss. Indiana Dune National Park and nearby sandy areas serve as a vital refuge for the species. The species can only be found in sandy habitats in early and mid-succession stage, and habitat management is an important tool to ensure a mosaic of successional stage (Smith et al. 2021). Therefore, more conservation efforts and habitat management practices should be implemented along Lake Michigan.

The other two species with G4 conversation status are *A. unipunctata* and *P. cursitans*. *Apterodela unipunctata* is a strict forest-dwelled species, as the adult inhabits shaded forests. The species has undergone habitat shrinkage in several states, but its population in Indiana is apparently secure

(S4) according to Natureserver. The species is not commonly collected probably because of collecting bias, as closed-canopy forest is not a common site for tiger beetle collection, combined with its cryptic coloration (Duran and Gough 2019). *P. cursitans* is another species with cryptic biology. MacRae et al (2011) found that the species is habitat specific and can only be found in bottomland forest along rivers with sandy clay loam soil in Missouri. The author also suggests that the population in Missouri may resemble populations in the Ohio and lower Mississippi River basins. Population in Indiana is also included in the range, so the species is expected to be found in similar bottomland forests, like the two sites in the southwestern boundary adjacent to Ohio River (see figure. 18) . The article suggests that the Missouri population is relatively secure, while the cryptic appearance, limited temporal occurrence, habitat specificity, and small size makes it hard to be found. More surveys should be conducted in suitable habitats to further corroborate their presence.

Besides species with conservation concern, a few species are rarely reported in Indiana. *Cicindela purpurea* used to be widespread in southern Indiana, but the species has not been reported since 1975. The species can adapt to various open habitats, and it doesn't require large intact habitats to sustain the population (Pearson et al. 2015). Also, the species cannot be misidentified to other species due to its unique appearance among all tiger beetles in Indiana. The only species that may be confused with it is *C. limbalis*, which doesn't have any record in Indiana (see discussion below). Interestingly, *T. virginica* and *C. pupurea* tend to share similar habitats, but *T. virginica* can still be found in many counties recently. Therefore, the lack of finding of the species is a mystery at this time. As suitable habitats of the species should still exist in the southern part of the state, extensive surveys may confirm its presence in the state.

Another rarely observed species is *E. cuprascens*. Recent records are all restricted to a single point in Clark county. The species are mainly found in sandy beaches along rivers and streams, so suitable habitats should still be abundant in southern Indiana. The absence of the species might be due to sampling bias, and future surveys should focus on its typical habitats. Similarly, *E. macra* may undergo apparent distribution shrinkage in Indiana. Current records show the species is only found in sandy areas along Lake Michigan. Historical records show that the species can reach as far south as Tippecanoe county, as well as other east and central counties (see figure. x) The species is currently listed as a state-vulnerable species (S3 status). As mentioned above, *E. macra* and *E. cuprascenes* are both found in two counties, while the records of *E. cuprascens* in the northern boundary and *E. macra* in southern boundary are mostly based on misidentifications. The similar appearance of the species makes them easy to be confused, so future investigation should carefully examine the specimen to confirm if two species overlap in Indiana. Pearson et al (2015) suggests the overlapped distribution of two species in Midwest, but recent occurrences of them are in two opposite boundaries of the state.

Another species occupying similar habitats is *C. hirticollis*, which used to have a relatively wide distribution in Indiana. Recent records of the species are rare and all concentrated in Indiana Dunes National Park. The species is generally susceptible to human activities and habitat alterations, like pollution, pesticides, river damming, channelization, and shoreline development. Many populations have disappeared in New England and Midwest (Pearson et al. 2015). A study of tiger beetles from southern Ohio (Kritsky et al. 1997) claims that the species may be extirpated from Hamilton county, where considerable destruction of shoreline was observed. A later study by the author concludes that the species in Ohio is only restricted to an approximately 25 mile stretch along Lake Erie, and the main causes of population decline are habitat alterations from road construction, flood control, irrigation, and development (Kritsky et al 1999). Similar cases might happen in historical sites of southern Indiana, where several major dams were built in the 20th century, accompanied by other modifications. Currently the species conservation status in NatureServe is "apparently secure (S4)" in Indiana. Compared with *E. lepida*, a species with almost the same current distribution as *C. hirticollis* in Indiana, *C. hirticollis* has fewer records along Lake Michigan. The species is also more vulnerable to larval habitat destruction by large vehicles and

other modifications, while *E. lepida* larvae *are* not apparently affected by them (Smith et al. 2021). If *C. hirticollis* is not found in other sites, the species should be evaluated as vulnerable, or S3 status, at least the same level as *E. lepida* and *E. macra*.

Doubtful species distribution

Despite our broad sampling, we still found no record for three species. *Cicindela ancocisconensis* is a species with conservation concern that used to be widespread in the midwest. Wilson and Larochelle (1980) points out old records of the species are known from Indiana, northern Illinois, and western Missouri. Pearson et al (2015) also suggests its historical records along the Ohio River, but probably extirpated now. However, the records in Indiana might be based on misidentifications. Blatchley (1910) lists the species in his book about Indiana beetles, but all specimens he collected were checked by us, finding that they are all misidentifications of *C. duodecimguttata*. Goldsmith (1916) also reported its occurrence in several localities, but we have not yet located his specimens. The species absence in Indiana might be due to lack of mountains as suitable habitats, and the records in Illinois, Missouri, and Ohio need to be confirmed.

Another interesting pattern is the doubtful presence of *C. splendida* and *C. limablis* in Indiana. Two species have confirmed records in Ohio, Kentucky, and Illinois. Bousquet (2012) includes indiana as the distribution range of both species, while Pearson et al (2015) shows the potential distribution of *C. splendida* in southern Indiana but doesn't include *C. limbalis*. In Schincariol and Freitag's (1991) revision of *Cicindela splendida* Hentz group, the map includes distribution of *C. splendia* in southern Indiana and probably the occurrence of *C. limbalis* in the northwestern corner. However, our data does not include any record within the state. The two species are both associated with red clay soil. The habitat specificity of two species may explain their absence in the state. While clay soil may still be present in the southern and eastern part of the state, we hope future surveys can find the species, confirming their distribution in Indiana.

Seasonality

Two distinct seasonality patterns were observed for tiger beetles in Indiana. The first pattern is characterized by a single-peak occurrence, where species occurrences are concentrated within several continuous months, with a dramatic decrease in abundance before or after this range. This pattern can be further classified into two subcategories: spring-occurring species and summer-occurring species. Spring-occurring species are rare, with *C. sexguttata* being the sole species exhibiting this pattern (see Fig. 6). Occurrences typically commence in March, peak in May, and decline significantly thereafter. In contrast, summer-occurring species are more prevalent, including *C. punctulata, C. rufiventris, C. hirticollis, C. formosa, T. virginica,* and potentially *C. patruela*. Some species have short occurrence periods, like three *Ellipsoptera* species (Fig. 7) and C. rufiventris (Fig. 5), which reach their highest occurrences in mid summer. Others, like *C. formosa* (Fig. 3), *C. punctulata* (Fig.6), *C. hirticollis* (Fig. 4), and *T. virginica* (Fig. 1), have longer occurrence periods, spanning from spring to early autumn.

The second observed pattern is characterized by double-peak occurrences, where species exhibit the highest occurrences in two distinct time periods, with low occurrences between them. This pattern, sometimes referred to as the spring-autumn pattern (Pearson et al. 2015), is observed in species such as *C. scutellaris, C. purpurea, C. duodecimguttata, C. repanda,* and *C. tranquebarica* (Fig. 2). However, it is noted that some species may exhibit a single-peak pattern with an extended occurrence period, and the low number of occurrences between two peaks may be attributed to sampling bias. Species such as *C. trifasciata, C. marginipennis,* and *P. cursitans* were not included

in the seasonality analysis due to their limited records in Indiana.

Finally, two species show apparently different patterns: *C. duodecimguttata* and *A. unipunctata*. Data from iNaturalist shows the first peak of *C. duodecimguttata* in June, and the occurrences number is close to the second peak in September. Our data shows the first peak in April, and the number is much less than the second peak in August. Our data shows the second peak of *A. unipunctata* occurs in September, while iNaturalist data indicates that the species has a single-peak pattern, and September is near the end of the occurrence period. The inconsistencies observed in some species' patterns may be attributed to insufficient sampling. For instance, C. patruela and *A. unipunctata* were rarely encountered in our collections, limiting our ability to accurately depict their true seasonality patterns. Despite these discrepancies, most species in Indiana exhibited seasonality patterns consistent with those reported on iNaturalist, indicating typical seasonal trends across different areas.

It is noteworthy that different seasonality patterns are observed on some species sharing similar habitats. As mentioned above, *C. scutellaris* and *C. formosa* usually are found in the same habitats. *C. scutellaris* has a double-peak pattern, while *C. formosa* has the single-peak pattern. *C. scutellaris* occurs earlier than *C. formosa*, and its occurrences decline after *C. formosa* reaches the peak. *Cicindela scutellaris* reaches the second peak when *C. formosa*'s occurrence is declining. The crossed seasonality pattern probably indicates niche separation between the two species. *Cicindela formosa* is one of the largest tiger beetle species in Indiana, and previous observations show that it can prey on other tiger beetles (Pearson et al. 2015), which may include *C. scutellaris*. The apparent decline of *C. scutellaris* after *C. formosa*'s peak may represent the either direct or indirect suppression by *C. formosa*. Similar pattern is also observed on *C. hirticollis* and *C. repanda*. The two species occupy sandy areas near water. *Cicindela hirticollis* reaches the peak in July and April when *C. repanda*'s occurrence is lower, and *C. repanda* reaches the second peak when *C. hirticollis* occurrence significantly declines. Considering *C. hirticollis* is probably absent in many counties, *C. repanda* may have more occurrences during the two peaks. Generally, the different pattern emphasizes the complexity of species interactions within shared habitats.

Limitations and future expectations

Our data includes tiger beetle specimens from 89 counties, which covers almost the entire area of the state (see Fig. 21). Nevertheless, there are still two counties without any tiger beetle records: Rush and Blackford. Future research should survey the two counties to confirm the presence of tiger beetles, as surrounding counties all have tiger beetle records.

Collecting and observation bias is clearly evident in our data. There are several areas with extensive records (see Fig. 22), like Tippecanoe county, counties along Lake Michigan, Marion county, Brown county, and Monroe county. The abundant records from Tippecanoe county and Marion county are generally because of the presence of Purdue University and Indianapolis. Counties along Lake Michigan have sandy areas where multiple tiger beetle species present, serving as an ideal site for tiger beetle collection. Indiana Dunes National Park also attracts many visitors each year, including naturalists. Besides, tiger beetle research along Lake Michigan is relatively abundant. Brown and Monroe counties include large forested areas, like Morgan-Monroe State Forest and Yellowwood State Forest, which are common sites for insect collection. Indiana University is also located in Monroe county. In contrast, the eastern part of the state has much less sampling. Wayne and Clark counties have some collections, while the remaining part only have a few records. Although many eastern counties are dominated by agricultural fields, some natural habitats still remain in the southeastern part, where multiple tiger beetle species might be found. Preserved areas like Clark State Forest and Big Oaks National Wildlife Refuge are potential habitats for forest-dwelled species, like *C. patruela* and *P. cursitans*, even the doubtful extirpated species *C. ancocisconensis*. Counties

along Whitewater River may have more suitable habitats for *C. marginipennis*. Anyway, the eastern part of the state should be sampled more extensively in the future to improve our understanding of tiger beetles in Indiana.

In future research, it is most important to conduct more tiger beetle surveys in potential suitable habitats, with a particular focus on imperiled species such as *C. patruela, C. marginipennis, E. lepida*, and C. *hirticollis*. The accuracy of historical specimen identifications for *C. ancocisconensis* from Indiana, as reported by Goldsmith (1916) and potentially other collectors, should be verified. If confirmed, future surveys should focus on the collecting locality to verify if the species is still present. To ascertain the distribution of *C. limbalis* and *C. splendida*, surveys of clay soil habitats in the southern and eastern parts of the state are warranted. Additionally, we anticipate the discovery of *C. purpurea* within the state; if not found, future research may delve into the reasons for its absence, given its wide geographical range (From Pacific to Atlantic) and strong adaptation to various open habitats (grasslands, meadows, forest clearings). Lastly, we recommend the increased use of additional trap types in future surveys (e.g., pitfall, light), as they may be useful for detecting species with cryptic coloration or behavior, such as *A. unipunctata* and *P. cursitans* that are easily overlooked (Wirth, personal observations).

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Appendix

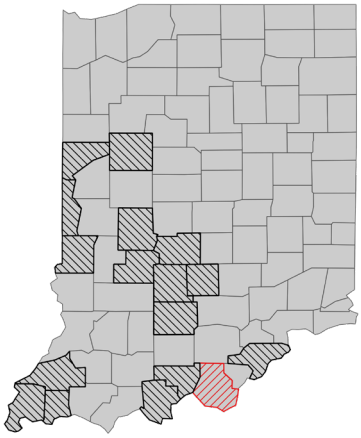

Fig. 1 *A. unipunctata*

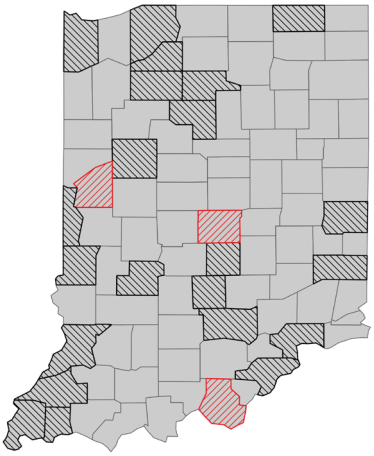

Fig. 2 *C. duodecimguttata*

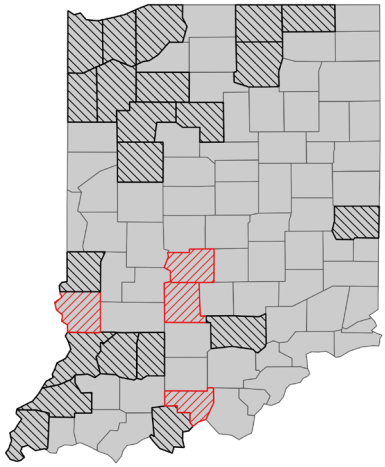

Fig. 3 *C. formosa*

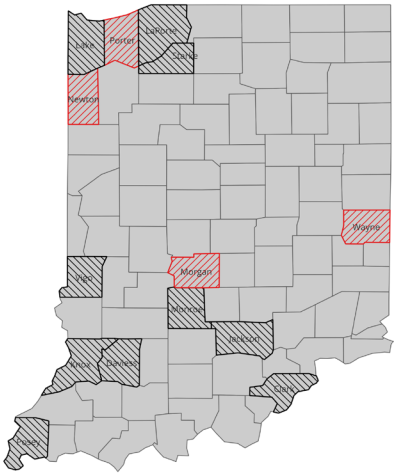

Fig. 4 *C. hirticollis*

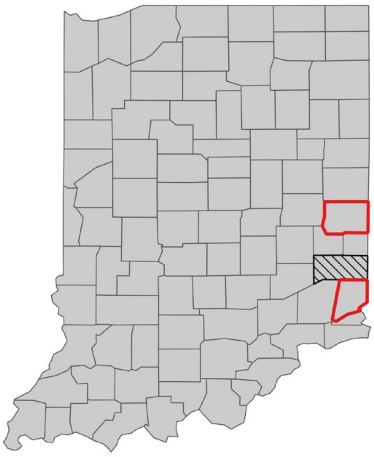

Fig. 5 *C. marginipennis*

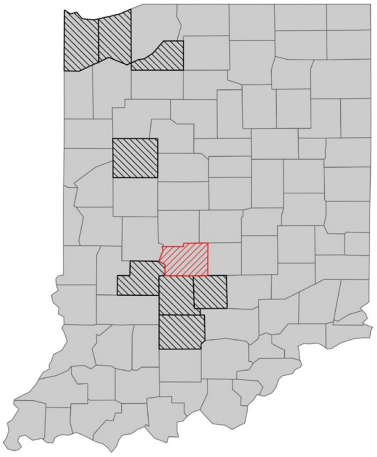

Fig. 6 *C. patruela*

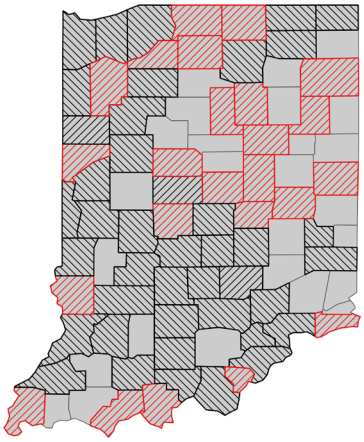

Fig. 7 *C. punctulata*

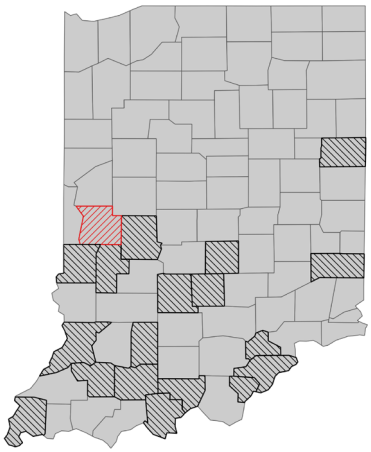

Fig. 8 *C. pupurea*

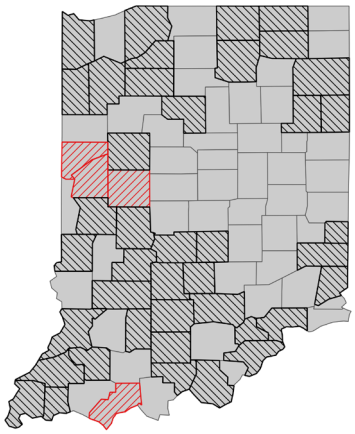

Fig. 9 *C. repanda*

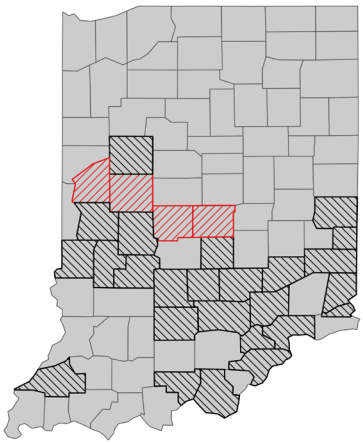

Fig. 10 *C. rufiventris*

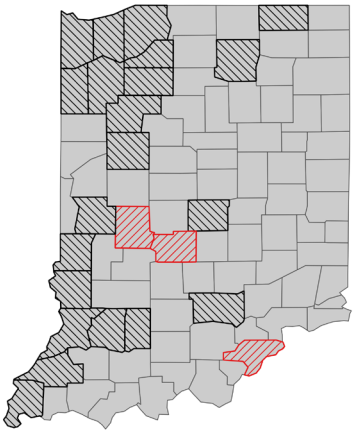

Fig. 11 *C. scutellaris*

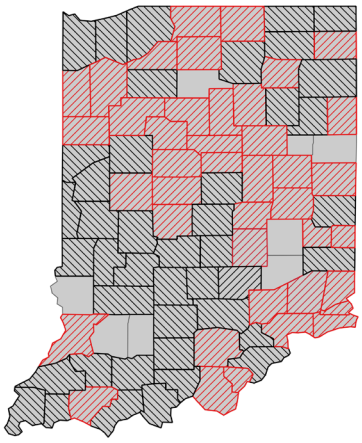

Fig. 12 *C. sexguttata*

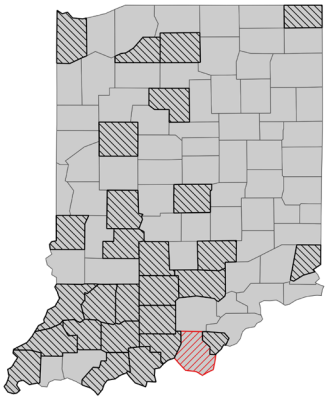

Fig. 13 *C. tranquebarica*

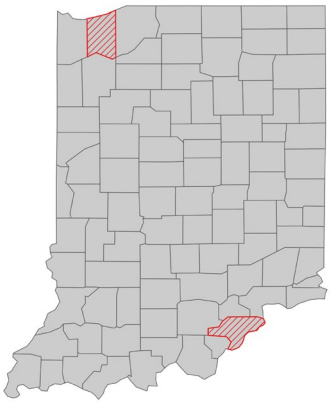

Fig. 14 *C. trifasciata*

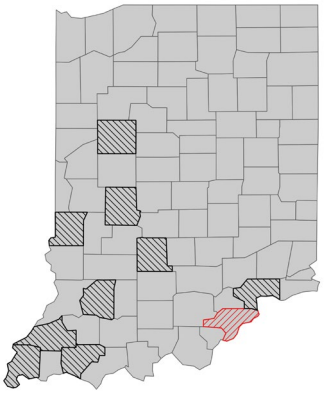

Fig. 15 *C. cuprascens*

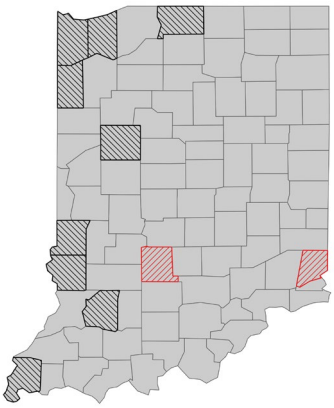

Fig. 16 *E. lepida*

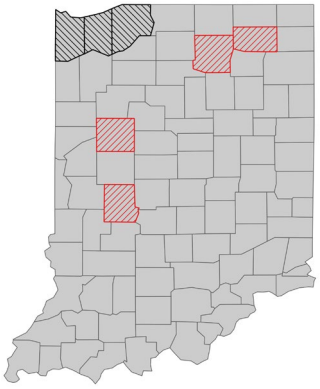

Fig. 17 *E. macra*

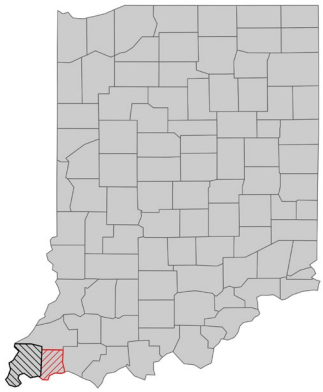

Fig. 18 *P. cursitans*

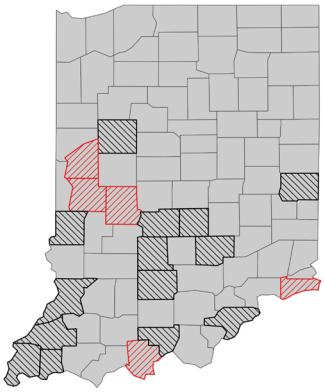

Fig. 19 *T. virginica*

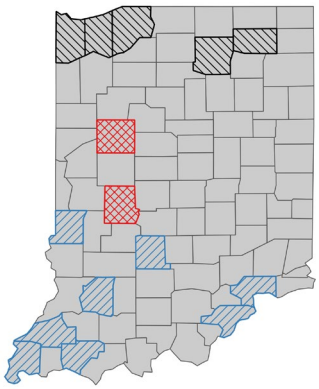

Fig. 20. Black slash-county with E. macra; blue slash-county with E. cuprascense; red cross-county with both species

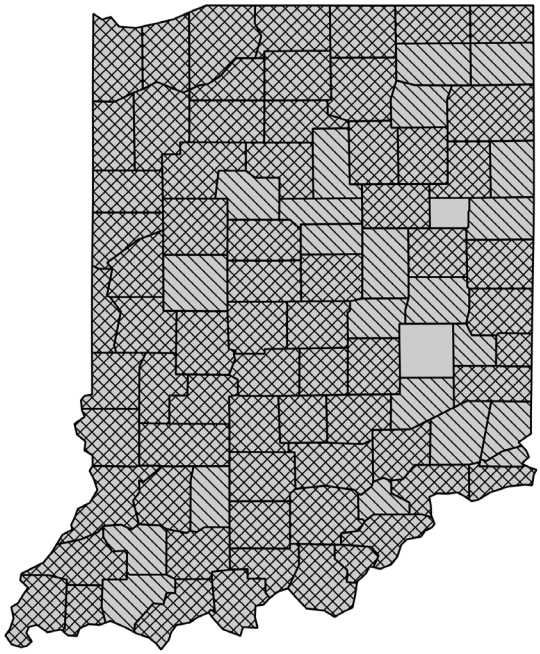

Fig. 21 All occurrences in Indiana. Cross-county with both PERC and GBIF records; slash-county with only GBIF records; blank-county without any tiger beetle records.

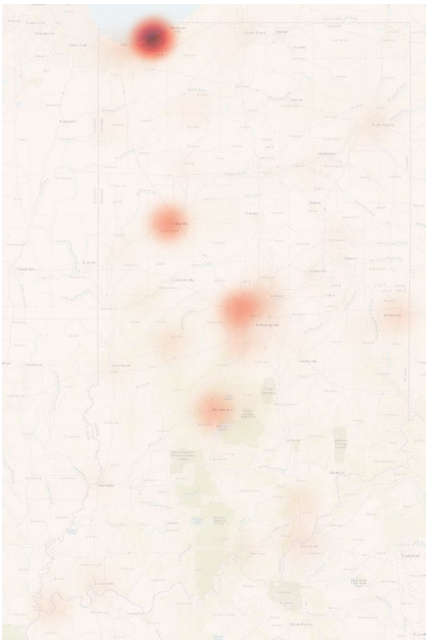

Fig. 22 Heat maps of all occurrences.

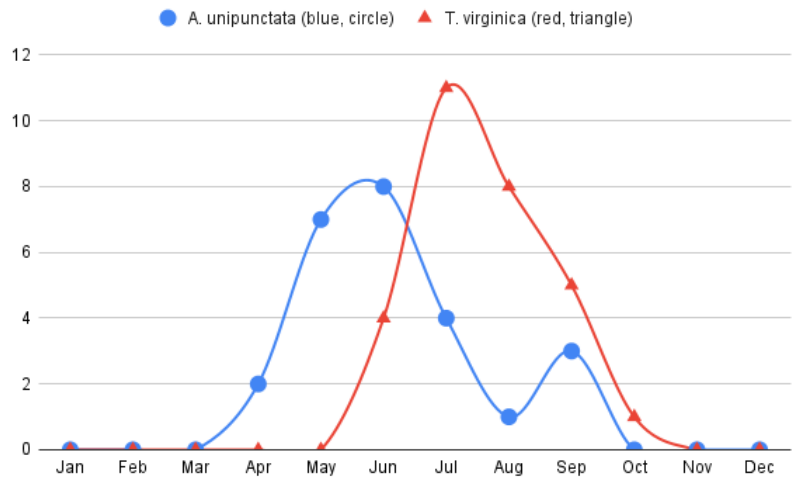

Chart. 1 Seasonality of *A. unipunctata* and *T. virginica.*

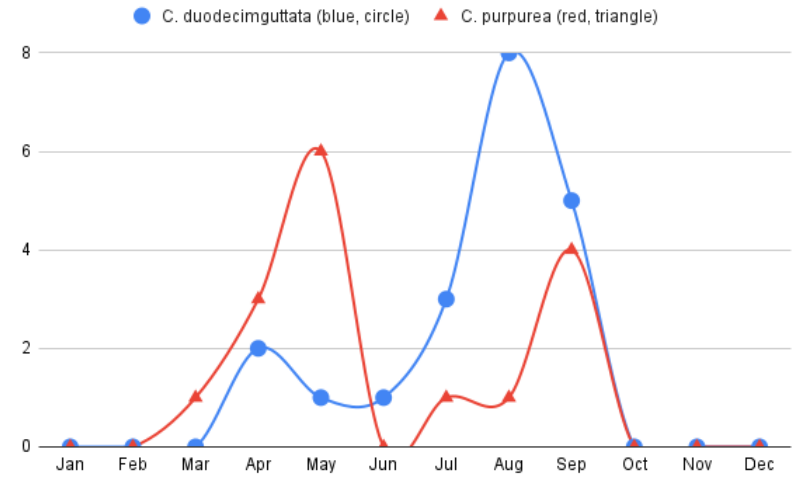

Chart. 2 Seasonality of *C. duodecimguttata* and *C. purpurea*.

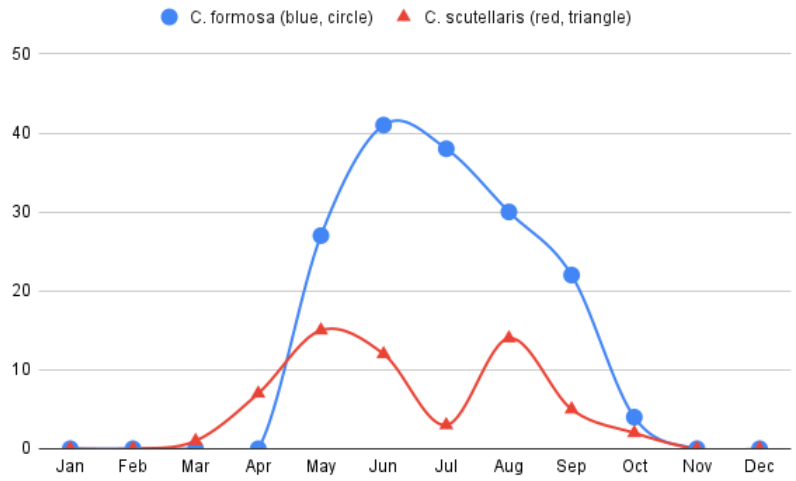

Chart. 3 Seasonality of *C. formosa* and *C. scutellaris*.

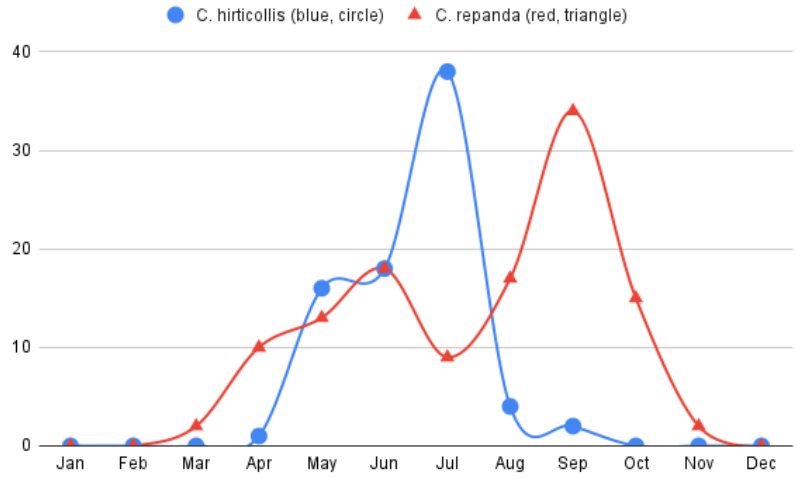

Chart. 4 Seasonality of *C. hirticollis* and *C. repanda*.

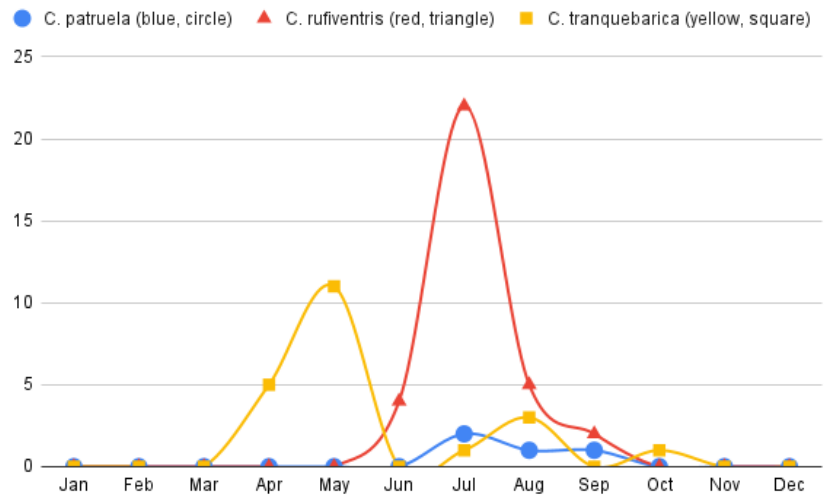

Chart. 5 Seasonality of *C. patruela*, *C. hirticollis*, and *C. tranquebarica*.

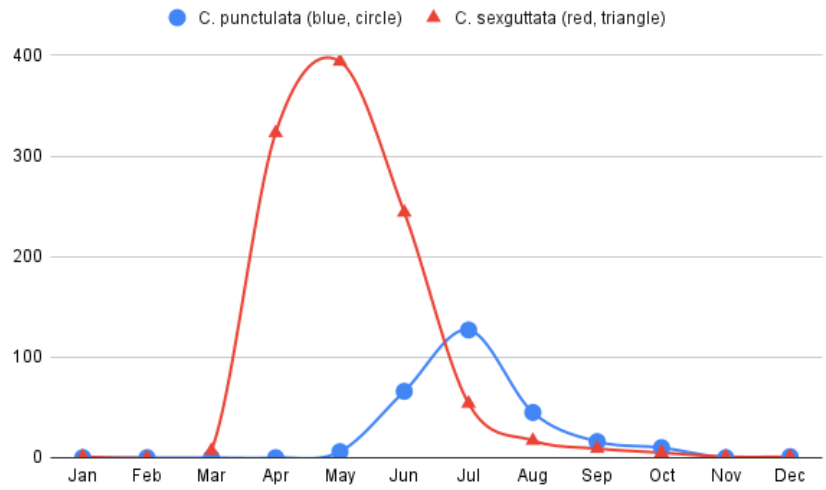

Chart. 6 Seasonality of *C. punctulata* and *C. sexguttata*.

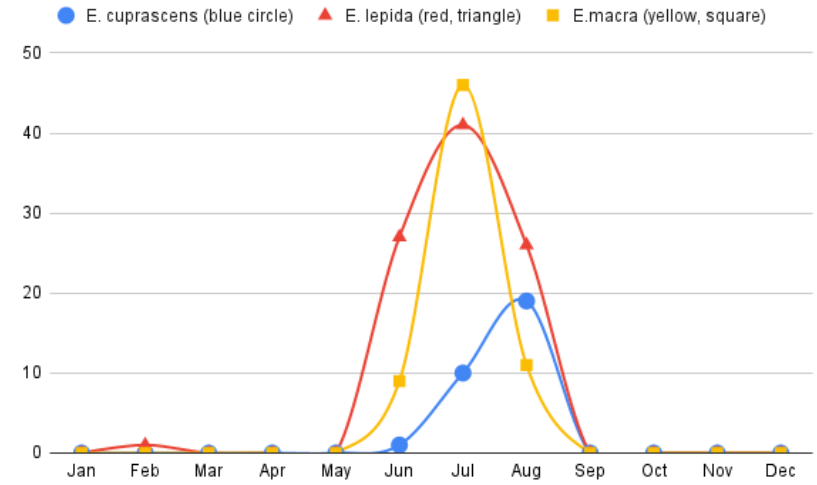

Chart. 7 Seasonality of *E. cuprascens*, *E. lepida*, and *E. macra*