The Biogeography of a Disjunct Plant-Insect Relationship: Thimbleberry and *Diastrophis kincaidii* (Hymenoptera: Cynipidae) in the Great Lakes Region

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Abstract

The clonal shrub thimbleberry (*Rubus parviflorus)* ranges throughout western North America and is disjunct to the northern Great Lakes region. *Diastrophis kincaidii* (Hymenoptera: Cynipidae) is an obligate gall wasp of thimbleberry that has long been known from western North America but has only been reported from the Great Lakes region since the early 1990s. It has been suggested that *Diastrophis kincaidii* was only recently introduced into the Great Lakes region sometime in the 1980s. We conducted a survey to determine the distribution of *D. kincaidii* and its parasitoids within the thimbleberry range in the Great Lakes region. We found that *D. kincaidii* is restricted to the colder and more xeric habitats within the Great Lakes thimbleberry range. Additionally *D. kincaidii* was found to have colonized isolated micro-habitats in the region were it attained high population densities. The inquiline community inhabiting *D. kincaidii* in the Great Lakes Region was similar to past reports. This community included species from eastern and western North America as well as two undescribed species. We suggest that *D. kincaidii* and its inquiline community have long been a part of the insect fauna of the Great Lakes region and is likely a remnant of an original connected pre-glacial continental thimbleberry population.

Diastrophus kincaidii Gillette (Hymenoptera: Cynipidae), is the only known gall maker of the clonal shrub thimbleberry (*Rubus parviflorus* Nutt.) (Weld 1957). The natural history and lifecycle of *D. kincaidii* was first described in the Pacific Northwest where it was originally thought that the wasp's range was restricted to the range of thimbleberry in western North America (Wangberg 1975). *Diastrophus kincaidii* females preferably oviposit on new first season thimbleberry shoots. Typically, eggs are communally deposited into the vascular areas of the plant stem. Galls form rapidly following oviposition, with the first evidence of swelling appearing in 5–7 days (Wangberg 1975). The occurrence of *D. kincaidii* in the Great Lakes region was confirmed by Kraft and Erbisch (1990). In their study, *D. kincaidii* was recorded from three counties in Michigan as well as Saint Louis county, Minnesota. Kraft and Erbisch (1990) also suggested, through the use of surveys by local botanists and berry pickers, that *D. kincaidii* arrived in the Great Lakes region sometime in the 1980s.

Although thimbleberry was first described from specimens collected from Mackinac Island, Michigan, Great Lakes thimbleberries are currently considered

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to be disjunct representatives of a larger population that extends from the coastal ranges of western North America into the Rocky Mountains (Voss 1985). In the Great Lakes region, thimbleberry has a fragmented distribution with clusters of plants occurring near Lake Superior and along the northern coasts of Lake Michigan and Huron (Marquis and Voss 1981). Many other Great Lakes disjunct plant species, for example black hawthorn (*Crataegus douglasii*), western fescue (*Festuca occidentalis*), and bilberry (*Vaccinium membranaceum*), exhibit similar distributional patterns (Marquis and Voss 1981). Thimbleberries are particularly abundant along Lake Superior's southern coast, even supporting a small commercial jam industry in the Upper Peninsula of Michigan (Anderson 2003).

Thimbleberry galls, like those induced by other cynipid wasps (Wiebes-Rijks and Shorthouse 1992, Gordinier 2003, Hayward and Stone 2005), are also inhabited by complex communities of insects (Wangburg 1976, Jones 1983). The most common members of this community are parasitoid wasps that attack *D. kincaidii* larvae. Thimbleberry gall communities have been described from western North America include members of the Hymenoptera families Inchneumonidae, Eurytomidae, Pteromalidae, Torymididae, Eupelmidae, and Ormyridae (Wangburg 1976, Jones 1983). Jones (1983) found that parasitoid presence selected for deeper oviposition within a gall in *D. kincaidii* and an increase in the number of females contributing to the formation of each gall. Parasitoids and gall inquiline communitites can change over a host species range, but they may also "follow" their host organism revealing ecological and phylogenetic affinities (Wiebes-Rijks and Shorthouse 1992, Schönrogge et al. 1995). Landscape patterns, environmental gradients, interspecific interactions, and host plant variability can all influence inquiline community composition (Kruess 2003). Kraft and Erbisch (1990) collected three unidentified parasitoid species from thimbleberry galls from the Upper Peninsula of Michigan indicating that Great Lakes region thimbleberry gall communities may be less species rich than those in western North America.

As in other *Rubus* subgenus *Anoplobatus* species, thimbleberry stems exhibit biannual growth patterns, first forming "primocanes" which become increasingly woody during year one and transform into reproductive "floricanes" in year two (Voss and Reznicek 2012). Gravid female *D. kincaidii* prefer to oviposit in the relatively soft, rapidly growing shoots of primocanes, which often host clutches of eggs from multiple female wasps (Wangburg 1975). Green, irregularly shaped galls form as larvae begin to feed during the first season and adults emerge from woody galls early in the summer of year two. Jones (1983) found that *D. kincaidii* larvae within larger galls and those that were deeper in these galls, had lower rates of parasitism.

The objectives of the present study were: 1) determine the range of *D. kincaidii* in the Great Lakes region 2) identify regional and local factors that influence the distribution of *D. kincaidii*, 3) describe the thimbleberry gall inquiline community in the Great Lakes region and 4) use new evidence to evaluate a previously published hypothesis regarding the history of *D. kincaidii* in the Great Lakes region.

Methods

We conducted a survey for *D. kincaidii* over the thimbleberry range in the Great Lakes region using our knowledge of thimbleberry stand locations and published distribution information from Marquis and Voss (1981), Reznicek et al. (2011), and Voss and Reznicek (2012) (Fig. 1). Surveys were conducted during the summer of 2013 from July to October after gall formation became apparent. Due to thimbleberry being rare and sometimes un-accessible in parts of its range, natural resource personnel from Parks Canada and the Nature Conservancy were provided with pictures of *D. kincaidii* galls and asked to survey local populations of thimbleberry in Bruce Peninsula National Park, Pukaskwa National Park

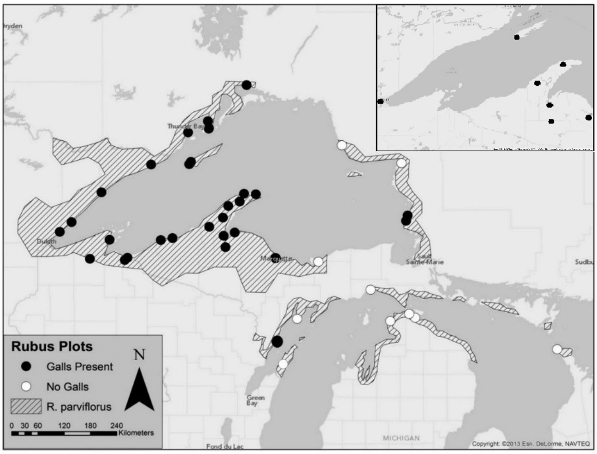

Figure 1. Distribution of *Diastrophis kincaidii* within the Great Lakes region. Range of thimbleberry based on Marquis and Voss (1981). Thimbleberry does not occur south of N 45°45' or east of W 81°30' in the Great Lakes region. Inset in top right is distribution as recorded by Kraft and Erbisch (1990) mapped at the county level. Note that the southern and eastern most points of Kraft and Erbisch's records were not verified and could not be re-located by Kraft and Erbisch.

(both in Ontario Canada) and Door County (Wisconsin) respectively. Surveys not conducted by the authors were recorded as presence/ absence (although no galls were observed in these areas) All thimbleberry stands surveyed (n = 103) in the region were mapped using ARCGIS (ESRI 2011).

At each stand (defined as a single clone separated by at least 10m from another nearby clone), we recorded the percentage of stems with galls and relative gall density. Variable width belt transects that ran the length of the thimbleberry stand were used to calculate the percent stems galled and relative density of galls for each stand. Each stem along the belt was recorded as either galled or ungalled and as either a floricane or a primocane. We also measured total stand area and calculated the ratio of floricanes to primocanes at each site.

A more intensive study of thimbleberry stands in a park in Marquette, Michigan was conducted to examine factors that influence local distribution of gall wasps. This area (46°33´12.03˝N, 87°24´22.08˝W) was surrounded by neighborhoods and a cemetery, forming an isolated forest remnant. The site is a 57 hectare area dominated by hemlock (*Tsuga canadensis)* and northern hardwood forests with several ruderal areas and recreational trails running throughout. We mapped and sampled all thimbleberry stands within the park to assess local variation in *D. kincaidii* abundance and density as well as to investigate spatial patterns on a local scale. Additionally, we mapped the recreational trails in the park to determine the influence of trails on local thimbleberry and *D. kincaidii* distribution.

A total of 88 galls were collected from the Michigan portion of the *D. kincaidii* range during August through October of 2013. These months covered the peak of thimbleberry growing season until the end of the growing season. Galls were cut from an individual thimbleberry stem when they had started to turn brown. Each gall was placed into a labeled jar, held at room temperature, and checked weekly for emerged wasps. Emerged wasps were identified as either parasitoid spp. or *D. kincaidii*. The gender of each emerged *D. kincaidii* was recorded and then it was prodded with a dissection pin (in order to provide initiative to flee as in Jones 1983) to see if they would fly in the lab. Parasitoid wasps were sent out for identification to genus (Roger Burks, Ohio State University, and Alexey Reshikov Swedish Museum of Natural History). Voucher specimen of *D. kincaidii* and parasitoids were deposited in the Northern Michigan University Insect Collection.

Data Analysis

To determine factors that influence variation in galler distribution at the local scale, distance to a hiking trail, distance to the nearest thimbleberry patch, and total density of stems, primocanes and floricanes were used as predictor variables for total gall density, percent stems galled in a patch and presence and absence of galls. Data collected from the intensive sampling site in Marquette Michigan were analyzed using non-parametric multiplicative regression (NPMR). NPMR avoids the unrealistic assumption of a simple linear or non-linear response of a response variable to a predictor variable (McCune 2006). HyperNiche version 2 (McCune and Mefford 2009) was then used to find the models that predicted gall density, percent of canes galled within stands and presence or absence of galls within a patch. Models were evaluated using a 100 iteration Monte Carlo randomization test and using xr^2. This metric uses a cross validation of the residual sum of squares in relation to the total sum of squares. Like r^2, xr^2 can be used to evaluate model quality.

Region-wide patterns were analyzed with simple descriptive statistics. We used the locations of Kraft and Erbisch (1990) to determine a potential spread rate of *D. kincaidii* within the Great Lakes region. Although Kraft and Erbisch (1990) was not a comprehensive range-wide survey for *D. kincaidii*, their work provided the best available starting point for assessing possible range expansion.

Results

Galls of *D. kincaidii* were found throughout the upper Great Lakes region, expanding the known range of *D. kincaidii* in the region as reported by Kraft and Erbish (1990) (Fig. 1). In addition to the known records, galls were recorded from Ontonagon, Menominee, and Marquette counties in Michigan; Iron and Bayfield counties in Wisconsin; Lake and Cook counties in Minnesota; and Thunder Bay and Algoma districts in Ontario (Table 1). Distribution of *D. kincaidii* within the Great Lakes thimbleberry range was clustered within the western portion of the Lake Superior watershed where galls were present in all stands surveyed. *Diastrophus kincaidii* was found as far east as Lake Superior Provincial Park in Algoma District, Ontario where two isolated occurrences were noted, and as far south as Menominee County, Michigan where a single isolated occurrence was detected (Fig. 1). Across the entire region in stands where galls occurred, an average of 16.7 ± 1.89% stems galled, and an average density of 1.62 ± 0.24 galls per square meter (n = 91). Only four (0.4%) of the 824 floricanes sampled were galled. *Diastrophis kincaidii* dispersal rate was calculated to be 19 km/year based on the presence of galls in the Duluth, Minnesota area in 1980, as reported by Kraft and Erbisch (1990), to the current location of Nipigon, Ontario, the furthest direct route of a new *D. kincaidii* record.

Nine parasitoid morpho-types (identified to genus) representing six Hymenoptera families were reared from the 88 field-collected galls (Table 2). These specimens represent parasitoid families previously collected from galls in in western North America (Wangberg 1976, Jones 1983). Wasps from these families also parasitize *Diastrophus nebulosus*, a gall former on *Rubus flagellaris,* which occurs in the lower peninsula of Michigan (Gordinier 2003).

Five parasitoid genera collected in this study have been previously collected from *D. kincaidii* galls from western North America (*Orthopelma, Eurytoma,*

Table 1. Average percent of stems galled and average density (per square meter) of galls for sampled geographic areas. Regional and state/provincial averages do not include counties or districts that had no galls present.

State/Province	County/ District	Average Percent Stems With Galls	Average Gall Density (m2)	n
Michigan		15.53 (±2.21)	1.33 (±0.26)	83
	Alger	-	-	3
	Baraga	12.45 (±5.65)	1.36 (±0.65)	4
	Cheboygan	-	-	2
	Delta	-	-	1
	Emmet	-	-	1
	Houghton	28.90 (±2.97)	5.06 (±2.2)	2
	Isle Royale	33.46 (±2.05)	2.39 (±0.74)	3
	Keweenaw	33.49 (±17.94)	3.76 (±1.5)	4
	Luce	-	-	1
	Mackinac	-	-	1
	Marquette	13.31 (±2.36)	0.99 (±0.27)	57
	Menominee	7.4 (±1.5)	0.56 (±0.23)	2
	Ontonagon	8.54 (±2.99)	0.83 (±0.16)	2
Minnesota		31.68 (±4.69)	5.75 (±1.11)	4
	Cook	30.77 (±11.33)	4.07 (±0.81)	2
	Lake	32.6 (±1.48)	7.43 (±1.05)	2
Ontario		19.07 (±3.50)	1.67 (±0.17)	11
	Algoma	8.54 (±5.47)	1.28 (±0.81)	3
	Manitoulin	-	-	2
	Thunder Bay	19.07 (±4.0)	1.87 (±0.75)	6
Wisconsin		27.26 (±5.15)	2.47 (±0.79)	5
	Bayfield	32.13 (±8.6)	1.87 (±0.44)	2
	Door	-	-	1
	Iron	22.39 (±6.17)	3.08 (±1.44)	2
Regional		16.7 (±1.89)	1.62 (±0.24)	103

Torymus, Eupelmella, and *Ormyrus*); Five have been found in *D. nebulosis* galls in southern Michigan (*Orthopelma, Eurytoma, Torymus, Eupelmella,* and *Ormyrus*); and two have not been previously associated with *Diastrophus* galls (*Xiphosomella* and *Pteromalinae*). The two members of Pteromalinae (Pteromalidae) are most likely un-described species (Roger Burks, Ohio State University, personal communication).

Thimbleberry covered approximately one percent of the total area of the intensively studied area in Marquette, Michigan (Fig. 2). *Disatrophus kincaidii* occupied 88% of the 57 thimbleberry stands examined. Gall density per stand was 0.99 ± 0.27 per square meter and thimbleberry plants covered approximately 2% of the park area. Thus we estimate that there were approximately 0.59 galls per square meter, or 3,430 galls in the park. Based on Jones (1983) average of 45 insects per gall this would put the populations of *D. kincaidii* for the park at an estimated 154,350 individuals. Average gall density per stand was measured at 0.99 ± 0.27 galls per square meter and on average 13.31 ±2.36% galled stems within stands. The best fit NPMR model indicated that presence/absence per stand was a function of distance to a hiking trail, density of primo canes, and floricanes density ($xr^2 = 0.25$, $p = 0.059$). Sensitivity analysis showed presence

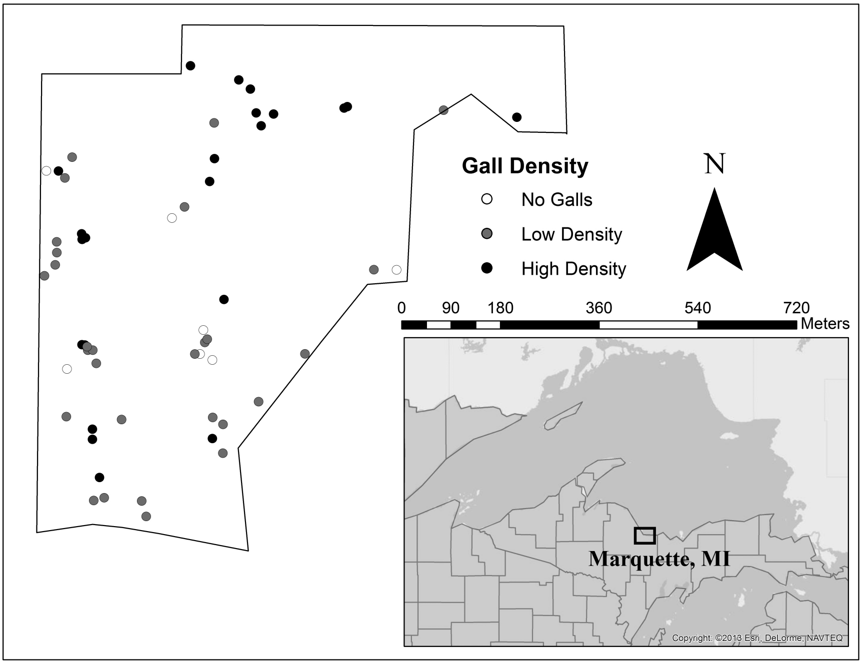

Figure 2. Patches of thimbleberry within the intensive locally sampled area in Marquette, Michigan with level of *Diastrophis kincaidii* galling for each patch.

was influenced most by distance to a hiking trail (sensitivity = 0.48) followed by lower flora cane density (sensitivity = 0.43) and an increase in primo cane density (sensitivity = 0.31). The model explained some of the variation in gall distribution within this study area, although it was only marginally significant and had low explanatory power. Both male and female *D. kincaidii* flew readily in the lab.

Discussion

Distribution of *Diastrophis kincaidii* in the Great Lakes Region. The results of our survey indicate that the present distribution of *D. kincaidii* in the Great Lakes region lies within the much larger range of its host plant, the thimbleberry, *Rubus parviflorus*, with most observations occurring in the western half of the Lake Superior watershed (Fig. 1). Following the regional micro-climate data from Fuller et al. (1995), the greatest densities of *D. kincaidii* galls, and the highest proportions of thimbleberry stems with galls, occurred in the coldest, driest habitats within the thimbleberry range, including apparently isolated gall wasp populations in relatively cold, dry environments in the eastern (Lake Superior Provincial Park, Algoma District, Ontario) and southern (Menomonee County, Michigan) parts of the survey area (Fig. 1). Interestingly, even within the heart of the *D. kincaidii* range along Lake Superior, a distinct density gradient was observed with greatest population densities occurring in the coldest, driest (more xeric) parts of the Keweenaw Peninsula, Isle Royale, and northeastern Minnesota, with densities decreasing where habitats within these areas become warmer and wetter (more mesic).

Table 2. Hymenopteran wasp communities found in *Diastrophus kincadii* galls in California (Wangburg 1976), and British Columbia (Jones 1983) and the present study. Also showing the hymenopteran gall community of *D. nubulosus* galls in southeastern Michigan (Gordinier 2003).

Family	California	British Columbia	Southern Michigan (*D. neubuosus*)	Great Lakes Region
Ishncumonidae	*Orthopelma californicum*	*Orthopelma californicum*	*c.f. Orthopelma sp.*	*Orthopelma sp* *Xiposomella sp*
Eurytomidae	*Eurytoma brevitergis*	*Eurytoma c.f. auriceps*	*Eurytoma diastrophus,* *Eurytoma rubrigalla,* *Tenuipetiolus ruber*	*Eurytoma sp.*
Pteromalidae	*Habrocytus sp.* *Artholytus sp.*	*Eryhromalus sp.,* *Arthrolytus sp.*	*Habrocytus sp.*	*Pteromalinae nsp #1* *Pteromalinae nsp #2*
Torymididae	*Torymus fagopirum,* *Torymus solitarius*	*Torymus fagopirum,* *Torymus solitarius*	*Torymus flavicoxa,* *Torymus advenus*	*Torymus sp. #1* *Torymus sp. #2*
Eupelmidae	*Eupelmella vesicularis,*	*Eupelmella vesicularis,*	*Eupelmella vesicularis*	*Eupelmella sp.*
Ormyridae	*Ormyrus sp.*	*Ormyrus sp.*	*Ormyrus labotus*	*Ormyrus sp.*
Eulophidae	*Tetrastichus sp.* *1 unknown*			
Cynipidae			*Synophromorpha sylvestris*	
Total observed	10	8	19	9

Gall position along a xeric-mesic gradient has been shown to strongly influence the survival of gall-forming insects as a result of increasing parasitism and fungal disease as habitats become more mesic (Fernandes and Price 1992). For example, Williams et al. (2003) exposed overwintering larval *Diplolepis* wasps (Hymenoptera: Cynipidae) to conditions simulating unseasonably warm winter weather and found that energy reserves required for pupation were depleted, which suggests that wasps overwintering in galls can be very sensitive to deviations from their optimal thermal environment. Like *Diplolepis* species, the super cooling point of *D. kincaidii* is quite low (-31.0 C to -40.0 C) (Ring and Tesar 1981) which suggests that the combination of this cold/xeric thermal optimum and (or) the sparse distribution of thimbleberry outside of the western Lake Superior watershed may contribute to the regional distribution patterns observed for *D. kincaidii*.

Local Distribution of *Diastrophis kincaidii*. The local distribution of *D. kincaidii* appeared to be random within and among thimbleberry stands in the intensively studied area. Predictive NPMR models showed mostly weak associations with different habitat variables, suggesting that within area groupings may be random for *D. kincaidii* on a local scale. Thimbleberry is a disturbance tolerating shrub (Camaeu et al. 2000) that can persist for long periods once established (Oleskevich et al. 1996). Many of the stands with galls present may have had very different characters when they were originally colonized by *D. kincaidii*. This could have masked some of the variables in the NPMR models.

Gall makers live in an intrinsically patchy environment, with preferred host plants often existing in a complex matrix of non-preferred plants and dispersal barriers. For instance, relative quality of plants may restrict cynipid gall wasps in local movements. Slight phenotypic difference in plants may create small "micro-populations" that are adapted to individual plants (Egan and Ott 2007). Since thimbleberry is a long-lived clonal shrub, *D. kincaidii* distribution may be highly influenced by between patch variability.

Despite the mostly random patterns of distribution there was still some explanatory power in the NPMR models. The model explaining presence/absence as a function of hiking trail distance and primocane and floricane density might also show how *D. kincaidii* patterns are influenced on a local scale. Hiking trails could affect colonizing *D. kincaidii* in several ways. First they may provide more areas on the outside of the thimbleberry patch that would make it easier for *D. kincadii* to encounter a thimbleberry patch when dispersing. Secondly, these trails may provide a corridor for dispersal. Lastly, disturbance along the trails, such as trail maintenance, may cut canes back and encourage the growth of primo canes which are selected heavily by *D. kincaidii* in preference of the second year floricane.

Emergent *D. kincaidii* search for new non-woody oviposition sites (Wangberg 1975), thus the relative density of primocanes may determine overall patch suitability. A large proportion of floricanes in a stand may reduce available oviposition sites and lower chances of gall induction. While stand area may approximate "target size" for dispersing *D. kincaidii*, it seems likely that primocane density is a more important determinant of habitat quality providing overall, more oviposition sites.

With an estimated *D. kincaidii* larval population in the intensive study area of 154,340 individuals, the population has a large pool of individuals. This large population size may lend itself to greater ability to spread locally though sheer numbers, maintaining regional populations. Chance dispersal increases with an increase in individuals (Simberloff 2009) and is most likely an important component of local distribution patterns in *D. kincaidii*. Despite the erroneous claim by Jones (1983) that female *D. kincaidii* are flightless, both male and females fly as observed numerous times in the present study. This fact greatly increases the potential for population expansion because ovipositing females are seemingly capable of short dispersal flights and also using flight to initiate passive atmospheric transport.

Community Ecology of the Great Lakes *Diastrophis kincaidii.* Gall making insects commandeer their host plant to produce large, nutritious organs (galls) that provide for larval development and in some cases, colonial existence. Like other forms of herbivory, the cost to plants of hosting gall makers can substantially reduce plant fitness by limiting the availability of resources required for growth and reproduction (McCrea et al. 1985, Abrahamson and Weis 1987). The effects of *D. kincaidii* galling on thimbleberries appear to include an additional structural constraint on sexual reproduction by limiting the future reproductive efficacy of the stems with galls.

The community of parasitoids found on *D. kincaidii* in the Great Lakes region have significant overlap with both the parasitoids found in the western North American part of *D. kincaidii* range and from the con-generic *D. nebulosus* in southern Michigan. In addition to this diversity of parasitoids from different geographic communities, the discovery of two undescribed species adds to the known diversity of the Great Lakes parasitoid community. Evidence gathered thus far indicates the *D. kincaidii* parasitoid community is a mix of a pre-glacial remnant community from a vicariance event with western North America, host switching from the southern Michigan associated species and possible (currently being described) endemism in the Great Lakes.

How Long Has *D.kincaidii* Been in the Great Lakes Region? Based on our estimate of the dispersal rate of 19 km per year, *D. kincadii* should have been able to reach any of the areas within the Great Lakes thimbleberry range since Kraft and Erbisch's (1990) study. Its occurrence on Isle Royale (Keweenaw County, Michigan) and several other seemingly isolated patches suggests that long-distance dispersal may frequently occur, perhaps by passive atmospheric transport initiated by dispersal flights.

Although little information exists about the dispersal rates of very small wasps, 19 km per year seems rapid when compared to other insects. For example, the invasion of a gall midge *Urophora cardui* (Diptera: Tephritidae) in Finland, proceeded at approximately 11 km per year (Jansson 1992). Although it impossible to rule out with currently available information, the present distribution of *D. kincaidii* appears to reflect a history in the Great Lakes region, perhaps similar to that of its host.

Diastrophus kincaidii is widely distributed in the Lake Superior watershed. Its relative abundance within the watershed creates a complex ecological system for studying multi-trophic interactions across biogeographical gradients. The interaction of *D. kincaidii* with one of the most recognizable plants of the Upper Great Lakes is a fascinating and important ecological relationship. Further studies will only reinforce our knowledge of plant insect interactions over broad and geographically disjunct regions, including studies to address niche shifts, interactions within and among trophic levels, environmental and biological factors that contribute to abundance, and how these factors influence that community composition.

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