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Habitat, dispersal, and distribution of the rare Orange-fruit Horse-gentian (*Triosteum aurantiacum* E.P. Bicknell; Caprifoliaceae) in northern Nova Scotia, Canada

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Abstract
Why some plant species are rare and how rare species persist are foundational questions in community ecology. In 2015 we repeated a 2006 survey of three river valleys in rural Antigonish County, northern Nova Scotia, Canada, which support populations of the rare herb Orange-fruit Horse-gentian (*Triosteum aurantiacum* E.P. Bicknell) to see how the populations had changed over a decade and to learn more about why the plant remains rare. Our survey confirms previous observations that Orange-fruit Horse-gentian is largely restricted to the understorey of hardwood and mixedwood stands, on bare ground within and near river floodplains, often with White Ash (*Fraxinus americana* L.). Predictive maps based on geographic information system modelling led to the discovery of new occurrences of the species along the three original rivers and along a fourth river, including a dense cluster in mature hardwood forest, which had not previously been considered habitat. Measurements of photosynthetic capacity using pulse-amplitude modulation (PAM) fluorometry showed significant stress on horse-gentian plants growing in full sunlight or light shade compared with plants beneath closed canopy confirming this plant is shade-adapted. Late-autumn observations of potential consumers of horse-gentian fruit suggest that White-tailed Deer (*Odocoileus virginianus*) may be the primary long-range disperser of seeds. Hence, this species may remain rare in northern Nova Scotia because its optimal habitat (mature, closed-canopy forest with open understorey and calcium-rich soil) is rare and distributed in disjunct patches (mostly along floodplains) and seed dispersal is limited by the range size of the deer.

Key words: Floodplain; GIS; rarity; shade tolerance; soil preference; White-tailed Deer

Résumé
La question de pourquoi quelque d'espèces de plantes reste rares et comment ils survivent en face de la compétition sont primordial en écologie. En 2015, nous avons répétées un levé de 2006 des populations de Trioste orangé (*Triosteum aurantiacum* E.P. Bicknell), une plante herbacée rare qui pousse dans les vallées de trois rivières dans la Comté d'Antigonish, au nord de la Nouvelle-Écosse, pour vérifier la grandeur des populations après neuf ans et comprendre pourquoi l'espèce reste rare. Notre levé a confirmé que l'habitat de Trioste orangé est presque limitée au sous-bois des peuplements feuillus et mixtes, sur sol nu, dans ou près des plaines inondables des rivières, et fréquemment avec Frêne blanc (*Fraxinus americana* L.). L'espèce ne se rencontre le long de deux autre rivières. Néanmoins, les cartes prédictives basées sur la système d'information géographique ont facilitées la découverte des nouveaux sous-populations de Trioste orangé le long des trois rivières originales et aussi le long d'une quatrième rivière, ça incluant un bouquet dense des plantes dans une forêt des feuillus matures, précédemment négligé. Comme mesurée par fluorimétrie, la capacité du photosynthèse de Trioste orangé poussant en plein soleil ou sous un ombre légère est réduite considérablement comparé à des plantes sous un ombre lourde, qui confirme que l'espèce est adapté à l'ombre. Des observations en automne de consomption des fruits de Trioste orangé suggèrent que Cerf de Virginie (*Odocoileus virginianus*) peut être le disperseur des semences primaire à longue distance. Donc, Trioste orangé peut reste rare au nord de la Nouvelle-Écosse parce-que leur habitat optimal (la forêt mature avec l'ombre lourde, sous-étage ouvert et sol riche en calcium) est lui-même rare, et distribué en carrés dissociés (la plupart des plaines inondables des rivières) et le dispersion des semences est limités par le taille de l'aire de répartition de Cerf de Virginie.

Mots-clés : plaine inondable; SDG; rarité; tolérance à l'ombre; préférence du sol; Cerf de Virginie

Introduction
A rare plant is one that has a low frequency of occurrence at some level of spatial resolution (Rabinowitz 1981). Why are some species rare and others common? How does the abundance of a rare species vary through space and time? More practically, to what

degree are rare species vulnerable to extinction and what steps can be taken to protect them? Although rarity does not invariably predict extinction, it can increase the probability of local or global extinction (Fagan *et al.* 2001; Matthies *et al.* 2004; Tscharntke and Brandl 2004).

The rarity of plant species has been shown in some studies to correlate with life history characteristics such as height, reproductive strategy, and number of seeds per fruit (Kunin and Shmida 1997; Eriksson and Jakobsson 1998; Hedge and Ellstrand 1999; Guo *et al.* 2000; Farnsworth 2007). An analysis of New England plants showed that rare taxa are more likely to be obligately insect pollinated, have short-range seed dispersal, and be near the northern edge of their range than more common species (Farnsworth and Ogurcak 2008). However, the only finding that was robust across studies in a meta-analysis of 54 life history studies of rare plants at different spatial scales was that rare species tend to produce fewer seeds than common ones (Murray *et al.* 2002).

These correlations provide insight into the characteristics typical of rare plant species, but they do not reveal why those species are rare, i.e., the ecological forces that keep their abundances low. Evolutionarily, rare species are often seen as less competitive than common species (Dawson-Markus *et al.* 2012), which has resulted in rare species evolving to occupy specialized niches in space (habitat) or time (phenology). Rare plant species are often restricted to rare habitats, such as lakeshores, serpentine soils, or alvars, where they are better adapted than more common species and can avoid competitors (Kruckeberg and Rabinowitz 1985; Baskin and Baskin 1988; Morris *et al.* 2002; Jeffrey 2003). These habitats are likely to be scattered in discrete patches within a matrix of non-habitat, creating the problem of dispersal from one patch to another. For plants whose seeds are dispersed by animals, habitat fragmentation may create barriers between used and unused habitat that some dispersers do not cross, limiting seed dispersal and colonization of new habitat (Rodríguez-Cabal *et al.* 2007).

The seed limitation hypothesis (Eriksson and Ehrlén 1992) suggests a plant's dispersal is limited by the number of seeds it can produce (source limitation) or the ability of the seeds to reach patches of suitable habitat (dispersal limitation). In contrast, the establishment limitation hypothesis (Clark *et al.* 2007) says that the primary limitation on the colonization of a plant species is the quality and number of microsites for establishment. These two hypotheses are related because a species limited to a few microsites would need abundant seeds or effective dispersal to guarantee colonization of new sites. Nevertheless, establishment limitation implies that a plant that colonizes a new site may not necessarily persist there if the site quality is poor, as Jacquemyn and Brys (2008) observed for understorey herbs on reclaimed agricultural land.

Orange-fruit Horse-gentian (*Triosteum aurantiacum* E.P. Bicknell; hereafter horse-gentian) is an uncommon, perennial herb that grows in rich deciduous forests of eastern North America. Plants are rhizomatous, each with multiple, pubescent, unbranched stems (up to 1 m) bearing pairs of decussately opposite, lanceolate leaves with wide petioles. Flowers are borne in the leaf axils. The fruit is a fleshy drupe, ~1 cm diameter, turning bright orange in autumn and containing three pyrenes (Roland 1998).

Triosteum aurantiacum is one of three North American *Triosteum* L. species that have overlapping distributions in the USA (Gould and Donoghue 2000) but the only member of the genus in New Brunswick (Hinds 1986) and Nova Scotia, where it grows at the northeastern limit of its distribution (Mazerolle *et al.* 2018). The species occurs in five Canadian provinces and 30 states, as far west as Nebraska and south to Georgia (USDA 2016). It is considered Vulnerable (S3), Imperilled (S2), or Critically Imperilled (S1) in seven eastern states, from Maine (DACF 2022) to Georgia (NatureServe 2023), and rare and Endangered in New Hampshire (NHDFL 2020).

Horse-gentian has long been considered a rare species in Nova Scotia (Mayer *et al.* 1978; Pronych and Wilson 1993) and is considered Vulnerable (S3) in both Nova Scotia and New Brunswick. Based on records held at the Atlantic Canada Conservation Data Centre, populations in Nova Scotia extend from northern Cape Breton south to the Meander and Herbert rivers, near Windsor, all on the north side of the province. The plant occupies upland forest in northern Cape Breton, but most other records in the province are from floodplains of 16 river systems. In no area is horse-gentian considered abundant, and historical observations, mostly in relation to medicinal plants, indicate it was never found in great numbers (Bigelow 1817; Barton 1818).

A previous survey of horse-gentian in northern Nova Scotia (Taylor and Tam 2012) revealed a patchy distribution along select river floodplains and a close association with White Ash (*Fraxinus americana* L.). Horse-gentian occurred primarily in areas of bare ground in regenerating hardwood forest but not in mature mixed forest or coniferous stands. The plant appears to favour partial shade but not dense underbrush or full sunlight. Taylor and Tam (2012) showed that horse-gentian prefers circumneutral soils, which is consistent with historical observations of it growing in limestone-rich areas (Bigelow 1817; Barton 1818) and its absence in acidic, spruce-dominated, upland forests.

Horse-gentian is an excellent candidate for studies of the causes and consequences of rarity in understorey plants. It has a large geographical range but occurs at low frequency in most places in its range. Although it grows in a variety of forest habitats in much of its range, in Nova Scotia it is restricted to specific habitats, mostly river floodplains and calcareous forests. While horse-gentian is uncommon to rare regionally, the plant is sufficiently abundant in suitable habitat patches to test hypotheses and support habitat modelling. Yet the species is absent from large areas of apparently suitable habitat along several river valleys in Nova Scotia, suggesting that a dispersal limitation perpetuates its rarity. The conspicuous fleshy fruits suggest zoochory, but while horse-gentian in northern Nova Scotia is restricted mostly to floodplains, most floodplains do not support horse-gentian, which suggests that the dispersal agent is either incapable of crossing ridges or does so infrequently. Determining the key species dispersing seeds would help answer this question. Studies on the factors limiting the distribution and abundance of horse-gentian may, in turn, shed light on the nature of rarity in plants generally.

The objective of our study was to assess the distribution, relative densities, and demographic characteristics (genet size, stem height, fecundity) of Orange-fruit Horse-gentian in Antigonish County to see how these population features have changed since the previous survey. From this information we sought to better understand the ecological causes of the plant's rarity. First, we resurveyed the three river valleys (Pomquet, West, South rivers) and other locations where Taylor and Tam (2012) reported finding horse-gentian in 2006 to see if those populations remained extant a decade later. To better understand the size and extent of the populations, we searched new areas of floodplain along two of these rivers (Pomquet, West) and added two others (Tracadie River, Brierly Brook) to look for plants that may have been overlooked before. We used these observations to create simple, predictive maps of habitat for the species along West River and previously unsurveyed Rights River. We then made ground searches based on these maps to efficiently search for more overlooked plants and to test whether our predictions of horse-gentian habitat were accurate. Second, we made demographic measurements of plants in three locations to test whether the quality of habitat could be inferred from plant size and fecundity. To test whether the occurrence of horse-gentian in young forest reflected a habitat requirement for light shade, we used pulse-amplitude modulation (PAM) fluorometry to assess the degree of stress experienced by plants growing in different habitats, from open ground to closed-canopy forest. Finally, we used motion-activated cameras and direct observation to identify organisms feeding on horse-gentian fruit, to address whether poor seed dispersal contributes to the patchy distribution of the species.

Methods

Population surveys

Between 16 June and 28 August 2015, we resurveyed horse-gentian populations surveyed by Taylor and Tam in 2006 (South River, Black Avon/Pomquet River, West River; Figure 1). We also surveyed upstream areas of West River floodplain not explored in 2006. The purpose of these surveys was to determine the relative abundance and size of the plants along each river and document the common habitat conditions in which they were growing.

We did not attempt to survey the entire length of these river valleys or to produce quantitative estimates of plant density. We surveyed 4 km along West River (mostly the north bank), 1.2 km along lower Black Avon River, 1 km along Pomquet River, and 1 km along South River (west bank), all within Antigonish County. We surveyed 1 km of lower Tracadie River in 2021. One observer cumulatively surveyed ~1 km of Brierly Brook, a major tributary of West River, from 2015 to 2020. Most survey sites lay within river floodplains but three survey sites along South River (Frasers Mills Upland, St. Andrews, Lower South River) and two sites along West River were in forests above the floodplain. The total area and number of sites surveyed along a river were determined by the presence of presumed habitat (young deciduous forest, sparse underbrush, bare ground) along the river and site accessibility. We attempted to survey the sites covered in Taylor and Tam (2012), using notes and coordinates from the earlier work, although changes to land cover (houses, thickets, channel shaping) since their surveys sometimes made that impossible.

We walked in pairs during the surveys, ~5 m apart, along a path parallel to the river or through upland habitat. When we found a horse-gentian, we marked its location with a global position system unit (Garmin eTrex Legend, Olathe, Kansas, USA) and recorded the number of stems, canopy cover, ground cover (along West and Pomquet rivers only), the identity of the two nearest trees, and the approximate distance from the river. We subjectively ranked canopy cover as open (1), mostly open (2), mostly closed (3), or closed (4). We recorded ground cover as bare ground, leaf litter, grass, moss, ferns, forbs, woody underbrush, or any combination of these. We noted damage to the leaves (insect damage, fungal growth) or the stems (deer browse, broken stems) of horse-gentian. Once all data were collected for a plant, we conducted a fine-scale search over ~10 m in all directions, seeking other individuals. If no more plants were detected,

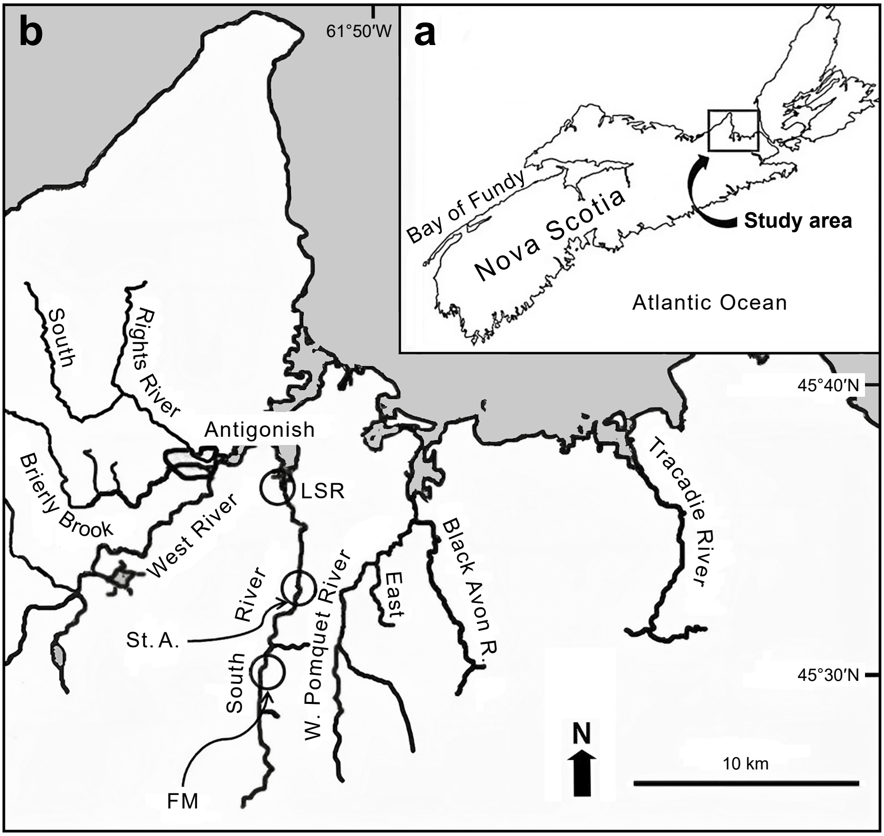

FIGURE 1. Maps of a. Nova Scotia and b. the rivers in Antigonish County surveyed for Orange-fruit Horse-gentian (*Triosteum aurantiacum*). Circles along South River indicate locations mentioned in the text: LSR = Lower South River; St. A = St. Andrews; FM = Frasers Mills.

we continued along the original line until the vegetation changed or no more horse-gentian was found.

At one site along South River and two sites along West River, where the channel was wadable, we crossed the river to determine if patches of horse-gentian on one bank extended across the channel. On most excursions, we also conducted brief surveys of presumed non-habitat (conifer stands, mature forest, areas of dense underbrush) next to presumed habitat.

We conducted demographic surveys on subsets of the horse-gentian populations along Pomquet River (25 genets, 115 stems), West River (13 genets, 95 stems), and Frasers Mills Upland (14 genets, 74 stems) from 13 to 30 September 2015. The Frasers Mills Upland data are part of a long-term study (B.R.T. unpubl. data). For each plant (genet) we recorded the number of stems, height of each stem, and number of fruits per stem. We measured stem height from the ground to the top of the apical buds. Each rhizome of Orange-fruit Horse-gentian produces a clump of stems (ramets) which collectively constitute the genet, the whole plant. Stems all arise from the same base, so it is easy to count the number of stems in each genet. We never encountered two plants so close together that the genets could not easily be distinguished.

Mapping

Using georeferenced locations of horse-gentian plants from the 2015 survey, we created predictive maps of horse-gentian habitat using ArcGIS 10.3 (ESRI, Redlands, California, USA). We acquired GIS files of forestry inventory data (NSDNR 2007) and soil survey data (AAFC 2010) and produced maps of the intersection, or areas of overlap, between soil types and forest types where the plants had been observed.

Field observations revealed a strong association between hardwood tree species and occurrence of horse-gentian (Figure 2), suggesting that hardwood forests would provide the best habitat. We defined forests as "predominantly hardwood" if they supported >70% hardwood species cover in forest inventory maps from NSDNR (2007). Areas containing

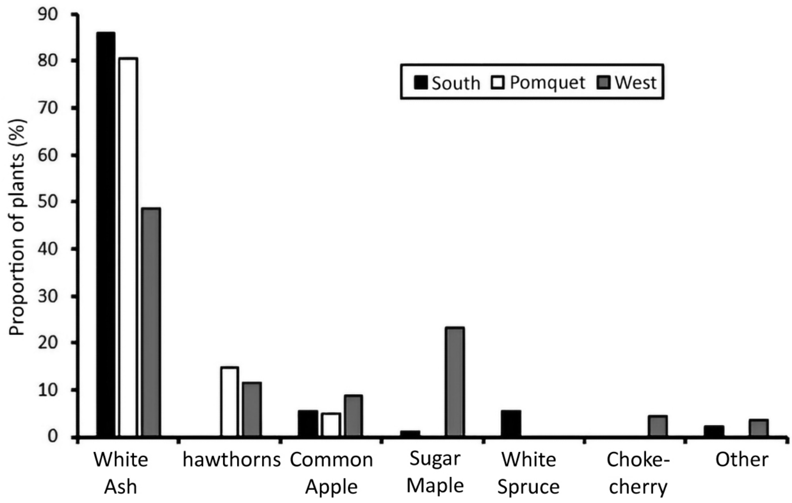

FIGURE 2. Nearest canopy trees to Orange-fruit Horse-gentian (*Triosteum aurantiacum*) genets along South, Pomquet, and West rivers in Antigonish County, Nova Scotia, in 2015.

>70% softwood (conifer) trees were classified as "softwood" and forest between these limits were classified "mixed forest". We mapped hardwood forests as potential horse-gentian habitat.

Examining the known locations of horse-gentian against the soils in the area showed that the plant has a high affinity (68% of georeferenced plants) for Orthic Humic Regosols (Entosols in the USDA classification), a weakly developed mineral soil formed from unconsolidated sediments that lacks a developed B horizon but contains an organic A horizon (Soil Classification Working Group 1998). Habitat for horse-gentian was then predicted to lie in areas of hardwood forest growing in Orthic Humic Regosols. Because these soils develop from fluvial sediments, they are concentrated in river valleys. Known locations of horse-gentian were also associated with flat to gently sloping land. However, slope was not included in the predictive GIS maps because it proved redundant with soil given that Regosols in the study area develop in floodplains.

We initially generated GIS-based, predictive maps for West, South, and Pomquet rivers. We undertook ground surveys to confirm occurrence of the plant in predicted locations along West River in 2015 (28–29 September, 5 October), 2016 (22 September), and 2017 (11–19 September, 19 October). In addition, anecdotal reports in 2018 suggested an un-surveyed population was growing along the floodplain of Rights River, which flows through the Town of Antigonish from the north (Figure 1). We created a predictive GIS map for Rights River using the same criteria as before. We undertook ground-truthing of those habitat predictions from 9 July to 20 August 2018.

Chlorophyll fluorescence

We used pulse-amplitude modulation (PAM) fluorometry to measure the quantum yield of photosystem II in selected Orange-fruit Horse-gentian genets as an index of photosynthetic efficiency and hence vigour of the plant. A low quantum yield could be a sign of stress and an indicator of a sub-optimal habitat (Murchie and Lawson 2013; Kalaji *et al.* 2016). Between 20 July and 3 September 2015, we measured quantum yield on nine genets (29 stems) from the lower Pomquet River floodplain and 19 genets (63 stems) from four sites in the South River valley. Two sites along South River (St. Andrews Upland, Frasers Mills Upland) were anomalous locations identified in Taylor and Tam (2012) where horse-gentian grows along the slope of the river valley, well above the floodplain. We paired these sites with floodplain sites (St. Andrews Floodplain, Frasers Mills Floodplain) directly downslope and <0.5 km distant. Two of the plants surveyed at Frasers Mills Upland had no canopy cover (because of recent forest harvesting), so we analyzed these separately to test for stress caused by lack of cover.

We estimated photosynthetic performance of horse-gentian leaves by measuring the maximum quantum yield of photosystem II, a measure of photochemical efficiency, using a portable PAM fluorometer (Diving-PAM, Heinz Walz, Effeltrich, Germany). We calculated maximum quantum yield as:

$$QY(II)_{max} = (F_m - F_o)/F_m = F_v/F_m$$

where F_o is the minimal value of chlorophyll *a* fluorescence in photosystem II in a dark-adapted leaf and F_m is the maximum chlorophyll *a* fluorescence of that leaf during a saturating flash, a non-modulated flash of light that fully reduces photosystem II. The difference between the minimum and maximum fluorescence values, F_m–F_o, is the variable fluorescence, F_v. Maximum quantum yield is therefore the ratio of variable fluorescence to maximum fluorescence; in unstressed leaves this value is consistently ~0.83 (Murchie and Lawson 2013). Stresses that influence photosynthetic performance may be reflected in lower values of F_v/F_m (Kalaji *et al.* 2016).

To measure quantum yield, we selected four leaves equidistant along each of 1–8 stems on each genet, to compensate for the effect of declining light intensity below the top of the plant. Portions of each selected leaf were enclosed in dark leaf clips and allowed to dark adapt for 10–15 min before measurements were taken. The intensity of the PAM fluorometer's monitoring beam, used to measure F_o, was 0.04 µmol photons/m^2/s, and the intensity of the saturating flash (0.8 s) was 10 000 µmol photons/m^2/s. We noted the health of the leaves, including colour, damage, and presence of fungi. Weather does not influence these measurements because the instrument measures the photosynthetic capacity of the leaf by subjecting isolated portions to flashes of light.

Dispersal agent survey

We set up motion-sensitive cameras with built-in flash (Wingscapes Wildlife Cam, Ebsco Industries, Birmingham, Alabama, USA; 8.0 MP, focal length 30 cm–infinity) facing relatively large genets (15 and 25 stems) above the South River floodplain at Frasers Mills on 17–19 October and 24–31 October 2015, when ripe fruits were abundant on the stems. We redeployed one camera to face the 25-stem genet from 5 November to 13 December 2015, after which snow cover was expected. Fruits do not persist over winter; they become soft and rot. We inspected photographs for the presence of animals near the plants or feeding on the fruits, which presumably would be dispersal agents. We tallied the number of days in which an animal was recorded near the plant and the number of distinct visits each species made.

Statistics

We compared canopy cover among the three river valleys using the χ^2 test. We compared stem height and number of fruits per stem (log-transformed) using one-way analysis of variance (ANOVA) followed by Tukey's test. Because fruits are borne in the leaf axils, number of fruits is correlated with stem height (r = 0.68, P < 0.001, n = 268). Therefore, we included stem height as a covariate in the ANOVA comparing fecundity among sites. We compared quantum yields among sites using a two-factor ANOVA on location and date, followed by Tukey's test. To avoid an unbalanced design, we averaged the results from the five stems with the highest quantum yields at each site and used these data to compare sites. Preliminary analysis revealed no significant difference (P < 0.05) in average quantum yield among leaf positions. Therefore, data from each site were not divided by leaf position. Statistical analyses used Statistix® v.10 (Analytical Software 2013).

Results

Population surveys

The survey of known horse-gentian habitat revealed that populations are more extensive and more dynamic than previously reported. We found 287 plants (1026 stems) along the three river floodplains in 2015 (Table 1). West River supported the largest population and Pomquet/Black Avon River the smallest. (Note: Pomquet River bifurcates near the mouth. The west branch is called West Pomquet River and the east branch is the Black Avon River but it is all the Pomquet River system; Figure 1.) Taylor and Tam (2012) reported only 96 plants in the 2006 survey, with the largest counts along Pomquet River and smallest along West River. We found horse-gentian 10 km further upstream along West River than Taylor and Tam (2012), in previously unexplored habitat (Figure 1). All the plants observed in 2015 in the Black Avon/Pomquet River system were growing along the Pomquet River main stem. We found no horse-gentian along either bank of Black Avon River, despite an extensive search, nor along lower Tracadie River or Brierly Brook.

Forays across South River revealed no horse-gentian on the bank opposite where the species was found. We did encounter horse-gentian along both banks of West River, but these patches were not

TABLE 1. Counts of Orange-fruit Horse-gentian (*Triosteum aurantiacum*) in each of three river valleys in Antigonish County, Nova Scotia, 2015, compared with counts from a 2006 survey.

Variable	Pomquet/Black Avon River	South River	West River	Total
Genets 2006*	66	22	8	96
Genets 2015	41	108	138	287
Stems 2015	207	394	425	1026

*Taylor and Tam (2012).

directly opposite each other.

We confirm that Orange-fruit Horse-gentian tends to grow in hardwood or mixedwood stands, closely associated with White Ash and to a lesser extent hawthorn (*Crataegus* L.) and Common Apple (*Malus domestica* (Suckow) Borkhausen). The plants we found along West River in 2015 sometimes occurred in more mature forest dominated by Sugar Maple (*Acer saccharum* Marshall; Figure 2). Among 179 plants for which we recorded ground cover, we observed bare ground around all but eight (96%), sometimes with cover of leaf litter or scattered grass and moss (Figure 3). We rarely found horse-gentian among other forbs, ferns, or woody underbrush.

Most horse-gentian plants were growing within a few metres of deer trails, as was noted in the 2006 survey. Of 287 genets recorded in 2015, 43 plants (15%) displayed truncated or broken stems, presumably caused by White-tailed Deer (*Odocoileus virginianus*) browsing. We noted insect damage on 150/287 plants (52%), although it was rarely severe. Conspicuous fungal infection was never observed.

Among 287 observations of tree cover above horse-gentian, almost half (45%) were in cover class 3, indicating mostly closed canopy. Virtually all the remainder was in cover classes 2 and 4. We found only seven plants (2.4%) in the open, cover class 1, and two of those were in recent clear-cuts. Median cover class was 3 overall, but cover class differed significantly among sites ($\chi^2_6 = 87.6$, $P < 0.0001$). Median cover class was 3 (mostly closed) along Pomquet and West rivers, but 2 (mostly open) along South River. Hence, plants along South River were exposed to more intense sunlight than in the other two river valleys.

Horse-gentian genets typically had one to three stems (Figure 4), with some individuals reaching 25 (South River), 32 (Pomquet River), and 55 stems (West River). The median number of stems/genet was two at South and West rivers, but three in Pomquet River, which had relatively fewer one-stemmed plants and more large, multi-stemmed plants (>10 stems; Figure 4).

Horse-gentian was found in substantial numbers at three upland sites along South River: Lower South River, St. Andrews, and Frasers Mills (Figure 1). The last two sites seem to be extensions of the populations in the floodplain; we consider all the plants in one river valley as a single population. The upland plants at Frasers Mills were growing in dense hedgerows and second-growth forest, often beneath apple trees. Median cover at this site was 3 ($n = 16$). The Lower South River site is an area of calcareous ground around gypsum outcroppings. The upland site at St. Andrews lies in a small (<1 ha) stand of White Ash, along the edge of a hayfield, and separated from the South River floodplain by a steep slope and a gravel road. The 2015 survey (in June) discovered 38 genets in this patch, compared with 35 in 2007. The median number of stems/genet was two in both surveys. The number of stems/genet was distributed almost identically between the two surveys (Figure 5). Hence, the population at this site appears to be stable.

Demographic data reveal that the West River population had significantly taller stems ($F_{2,282} = 12.78$, $P < 0.001$) than plants from Pomquet River or Frasers Mills Upland. Comparing the number of fruits per stem among sites, using stem height as a covariate, revealed a clear distinction among sites ($F_{2,281} = 45.5$, $P < 0.001$), with Frasers Mills Upland > Pomquet River > West River. Hence, plants in the thickets at Frasers Mills, just above the South River floodplain, were shorter but most fecund while plants along West

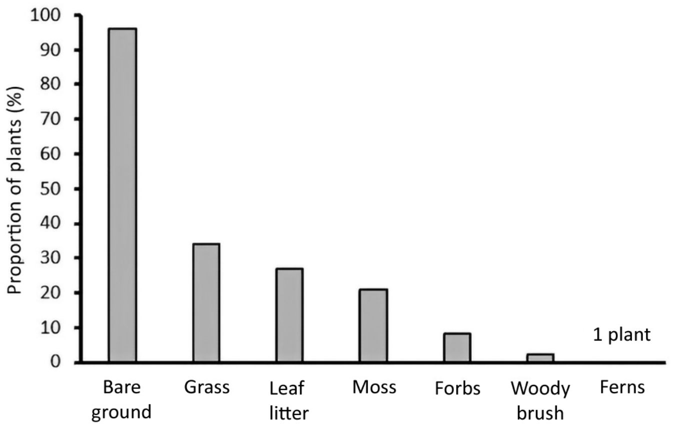

FIGURE 3. Distribution of ground cover around 179 Orange-fruit Horse-gentian (*Triosteum aurantiacum*) plants in South, Pomquet, and West river valleys, Antigonish County, Nova Scotia, in 2015. More than one kind of ground cover could surround an individual plant; therefore, columns do not add to 100%.

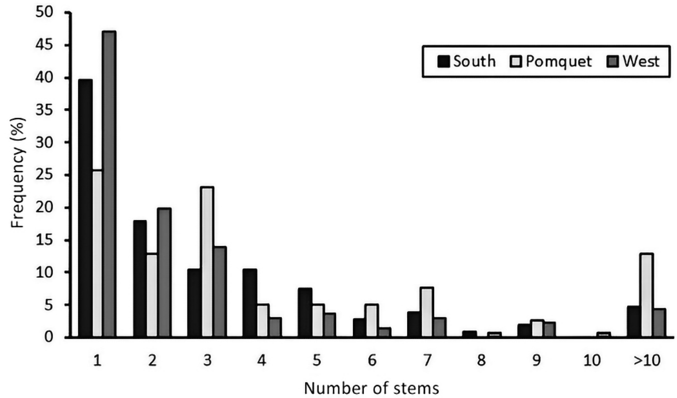

FIGURE 4. Distribution of number of stems/genet among Orange-fruit Horse-gentian (*Triosteum aurantiacum*) plants from South, Pomquet, and West rivers, Antigonish County, Nova Scotia, in 2015.

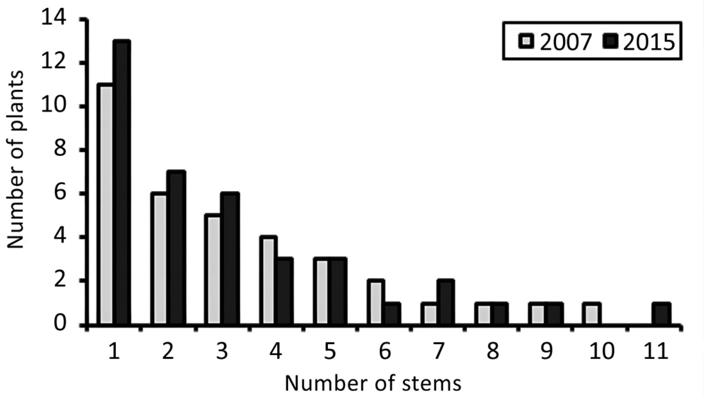

FIGURE 5. Distribution of number of stems/genet of Orange-fruit Horse-gentian (*Triosteum aurantiacum*) in a confined stand of White Ash (*Fraxinus americana*) along South River, near St. Andrews, Nova Scotia, in 2007 (Taylor and Tam 2012) and 2015.

River were taller but least fecund. The Pomquet River population was intermediate in both characters. In the 2006 survey, Pomquet River plants were both taller and more fecund than those in South River floodplain (Taylor and Tam 2012).

Habitat mapping

The GIS exercise revealed substantial areas of potential horse-gentian habitat along all three river valleys. As expected, potential habitat was mostly limited to the river floodplains, usually within a few decametres of the river channels. Habitat was distributed as elongate, linear patches interrupted by river sections running through steeper valleys where the floodplain was restricted. Occasional patches of potential habitat were revealed in isolated upland areas, especially near West River, and along wider tributaries to the main-stem rivers.

Ground-truth surveys of West River from 2016 to 2018 revealed over 200 plants at five new locations predicted by habitat mapping (Figure 6). Many of these plants were growing in places previously thought to be suboptimal habitat for the species, such as mature forest and mixedwood stands with numerous softwood trees. The species was abundant wherever it was found. We did not find horse-gentian at two predicted locations (Figure 6). One of these was a large alder swamp; the other was too dense with underbrush to constitute habitat.

The ground-truth survey in 2017 unexpectedly revealed one new patch of horse-gentian growing in mature hardwood forest on a steep slope ascending from the West River floodplain. This site is only ~200 m × 60 m, yet we recorded 141 Orange-fruit Horse-gentian in this small area. These plants were growing in an open understorey among large Sugar Maple (trunk diameter 24–68 cm, $n = 9$), White Ash (46–65 cm, $n = 2$), Trembling Aspen (*Populus tremuloides* Michaux;

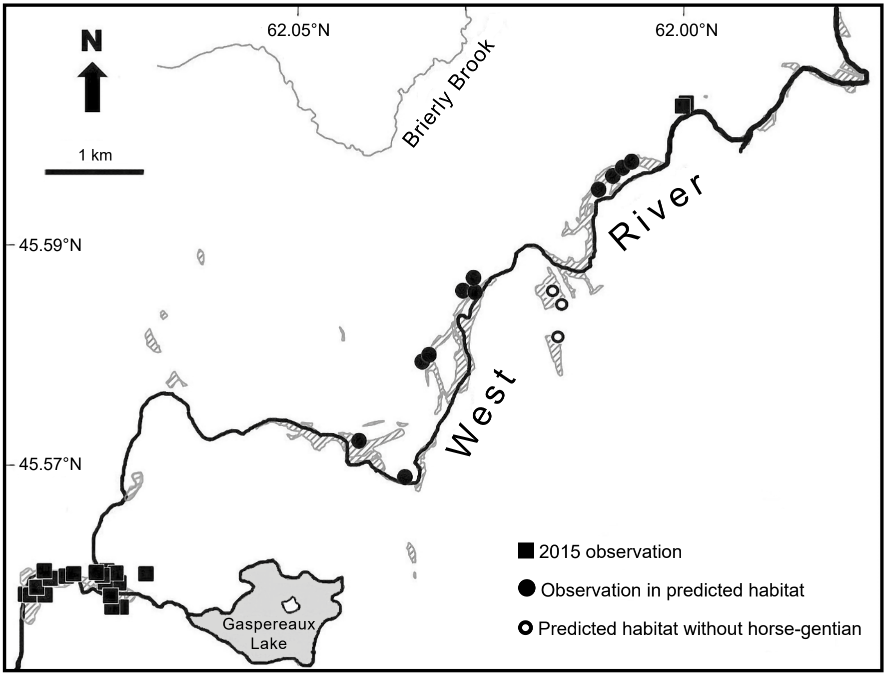

FIGURE 6. Map of West River, Antigonish County, Nova Scotia, showing predicted habitat (grey diagonal lined) for Orange-fruit Horse-gentian (*Triosteum aurantiacum*).

30–35 cm, $n = 6$), and American Beech (*Fagus grandifolia* Ehrhart).

The ground-truth survey of Rights River covered ~1.5 km along the South Branch (Figure 7). Horse-gentian was scattered throughout the surveyed reach and grew in such abundance that recording locations of all plants became impractical; we thus stopped doing so after the first 323 plants encountered. Plants along the east-flowing, lower reach (Figure 7) were growing in typical floodplain habitat, on flat ground dominated by young hardwood forest (White Ash, Sugar Maple, birch [*Betula* L.], and Chokecherry [*Prunus virginiana* L.]). Farther upstream, along the south-flowing channel, we discovered many plants on a steeply sloping hillside covered with mature, mixed forest of the above species plus White Spruce (*Picea glauca* (Moench) Voss) and Eastern Hemlock (*Tsuga canadensis* (L.) Carrière). Horse-gentian association with White Ash was strong at this site. Only 12/323 records of horse-gentian along Rights River do not report White Ash as one of the two closest trees. Median cover index was 3. Ground cover was universally bare ground with leaf litter.

Most horse-gentian plants along Rights River were short and appeared to be young. Over 80% of 323 genets recorded had only one (59%) or two (23%) stems (median one). Large, multi-stemmed plants were rare: only 4% of genets had >5 stems, compared with 12–27% in the other river valleys; the largest plant had 11 stems.

Chlorophyll fluorescence

Our analyses revealed a significant difference in the average quantum yields among horse-gentian populations at the sites surveyed ($F_{3,5} = 6.33$, $P < 0.001$; Figure 8). Quantum yields at four of the five sites were similar and close to the typical value of 0.83. Quantum yields of plants at the upland St. Andrews site, a compact group of 38 plants in a stand of White Ash and not in the flood plain, showed no significant difference from the floodplain plants downhill from them, nor from floodplain plants along Pomquet River. Surprisingly, mean quantum yield of plants at the Frasers Mills Upland, a scattered group of plants growing in hedgerows and second-growth forest and not in the flood plain, was significantly greater than that of plants growing in the forested floodplain below (Figure 8). Floodplain plants at Frasers Mills had the lowest quantum yield of any shaded site. Mean quantum yield of plants lacking tree cover at Frasers Mills Upland was also significantly less than shaded plants at the same site (Figure 8), confirming that Orange-fruit Horse-gentian is a shade-adapted species.

Dispersal agent survey

The field cameras caught White-tailed Deer near

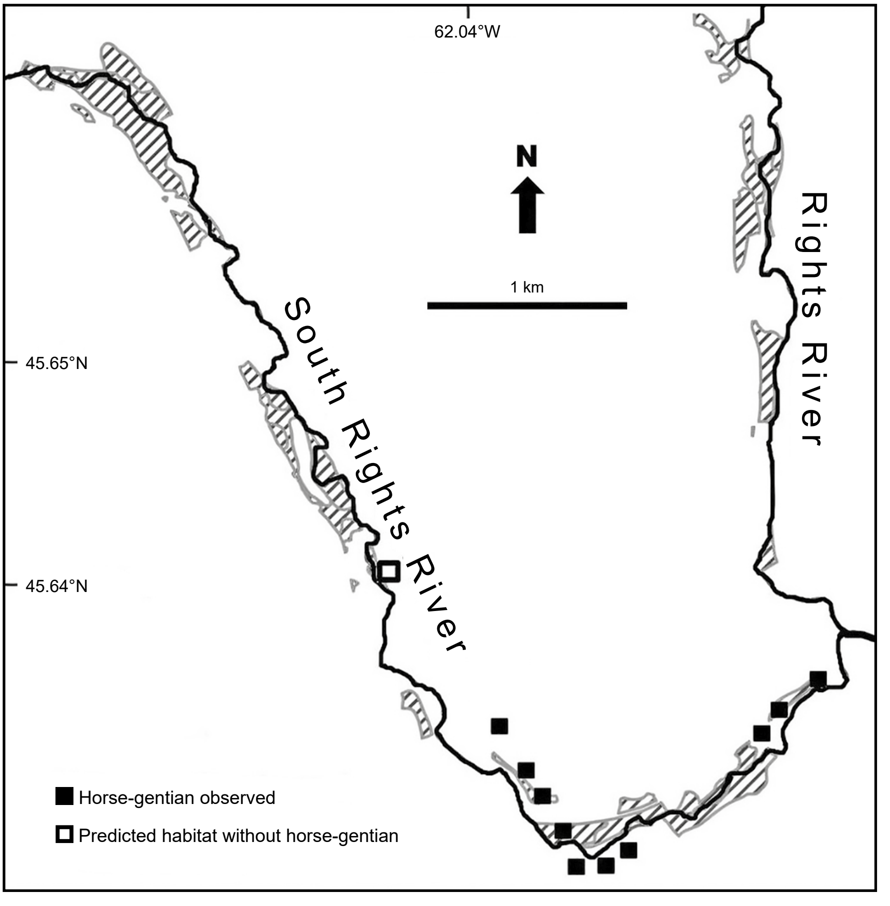

FIGURE 7. Map of lower West Branch, Rights River, Antigonish County, Nova Scotia, showing predicted habitat (grey diagonal lined) for Orange-fruit Horse-gentian (*Triosteum aurantiacum*).

horse-gentian on seven days (eight visits). Although not the most frequent visitor, the deer showed great interest in the plant, and some photo series show clear foraging behaviour, indicating that deer were consuming the plant with the attached fruits. Snowshoe Hare (*Lepus americanus*) was photographed on the most days (12 days, 20 visits). An Eastern Chipmunk (*Tamias striatus*) was photographed on two days, and in one picture its cheeks are full, an indication that it had been foraging. The other mammalian captures were Raccoon (*Procyon lotor*) and North American Porcupine (*Erethizon dorsatum*), which were each seen on two days (two visits each). The only birds captured were a Black-capped Chickadee (*Parus atricapillus*) and an American Robin (*Turdus migratorius*), which were each noted in only a single visit.

Damage apparently from deer browsing was observed on multiple plants over the course of the survey, at one or more sites along each river. Deer damage was seen on 8% of Frasers Mills plants, 6% of Pomquet River plants, and 50% of West River plants. Fruits were observed on the stems well into the fall, also suggesting distribution by foraging animals. Deer and deer tracks were commonly observed at the Frasers Mills Upland site and in all river valleys during our research, showing that deer are common in known horse-gentian habitat.

Discussion

Our study revealed new information about the distribution of Orange-fruit Horse-gentian in northern Nova Scotia and about some factors limiting that distribution. Horse-gentian grows primarily in closed canopy hardwood or mixed forest with open ground and Orthic Humic Regosol soil. These conditions occur most often in river floodplains. However, its occurrence well above the floodplain in Frasers Mills and St. Andrews and far upslope from Rights River demonstrates that the restriction to Regosol is not absolute. Soils at these upland sites are Orthic

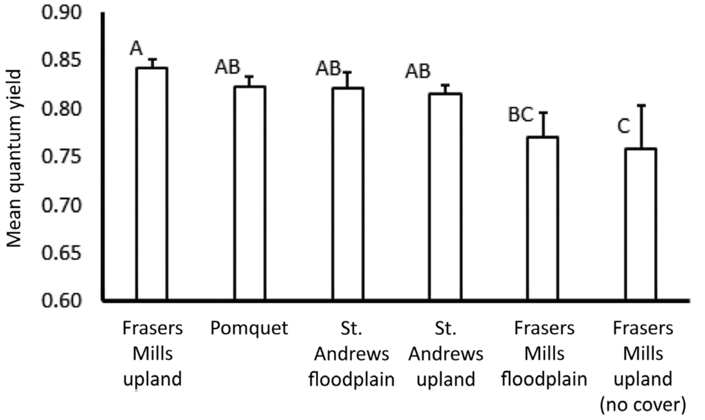

FIGURE 8. Mean quantum yield of chlorophyll in leaves of Orange-fruit Horse-gentian (*Triosteum aurantiacum*) from different habitats along South and Pomquet rivers, Antigonish County, Nova Scotia. Treatments sharing the same letter are not significantly different (Tukey's test, $P < 0.05$). Error bars are SD. Plants in Frasers Mills Floodplain are significantly more stressed than those in the upland nearby; a plant deprived of shade by forest harvesting shows significant stress compared with shaded plants. Unstressed leaves consistently have a value of ~0.83 (Murchie and Lawson 2013).

Humo-Ferric Podzols (USDA Cryorthod or Haplorthod), by far the most common soil type in northern Nova Scotia (AAFC 2010). Humo-Ferric Podzols, developed over unsorted glacial till, are rich in organic matter but highly leached, acidic, and nutrient poor. Evidently, horse-gentian may be catholic in its soil preference if other conditions are suitable.

In appropriate habitat, the species appears to be more abundant and widespread than previously documented in Nova Scotia. We discovered many more plants along South River and West River than in the 2006 survey. This increase was partly because we surveyed a larger area; apparent distributions of rare species are strongly influenced by search effort (Kadmon *et al.* 2004) and ease of access (Keith 2000). We found plants along West River growing 10 km upstream, beyond the previously known extent of the population and sometimes in places that would not previously have been considered habitat for the species. The same may be said for the population growing in mature, closed-canopy forest along upstream Rights River.

In contrast, the total plant count for the Pomquet/Black Avon River system was lower in our survey than in 2006 because we found no horse-gentian along Black Avon River, where Taylor and Tam (2012) found 20. Our survey was guided by location data and notes from Taylor and Tam (2012) but also covered a larger area along the floodplain. While a survey can never prove the absence of the target species, a sharp decline in the number of horse-gentian plants along Black Avon River is evident. The underbrush (mostly thickets of Chokecherry) had grown denser along both the Pomquet and Black Avon rivers in the nine years between surveys, making the floodplain difficult to search and perhaps reducing habitat quality for horse-gentian. Floodplain forests in Antigonish County have developed on abandoned farmland (Gentilcore 1956). Early successional stages on this land often develop dense thickets of Chokecherry and other short-lived tree species, which may be detrimental to horse-gentian.

Where horse-gentian occurred it was usually relatively abundant, and all other local populations appear to be stable in number or growing. Despite the loss of the species along Black Avon River, the frequency of its occurrence along the floodplains of South and Pomquet rivers did not noticeably change between the two surveys. However, the Pomquet River population had more large plants (more stems) and fewer single-stemmed (presumably younger) ones than populations along the other rivers, which suggests poor recruitment; fecundity at this site appears to have declined compared with 2006 (Taylor and Tam 2012). The size of the population above the floodplain at St. Andrews has remained stable (35–38 genets) for a decade. Size and fecundity of the plants at Frasers Mills are assessed every autumn in a long-term study (B.R.T. unpubl. data); that population also appears to be slowly increasing.

Ground-truth surveys suggest that predictive habitat mapping based on forest cover and soil type was generally successful in identifying potential habitat. These maps indicate scattered, often elongated, patches of habitat along all the surveyed rivers and some tributaries. Perhaps because the maps were extrapolated from surveys of river valleys, they do not predict occurrences in upland areas, where the species was also sometimes encountered. For example, while GIS-generated maps correctly predicted habitat along the floodplain of lower Rights River (South Branch), they failed to predict the extended population throughout the hillside forest farther upriver.

The application of GIS to locating horse-gentian in Antigonish County provides the basis for a general approach to surveying occurrence of rare plants when some aspects of the environment and community structure are known (Sperduto and Congalton 1996; MacDougall and Loo 2002; Draper *et al.* 2003; Neigel *et al.* 2022). For Nova Scotia and most of southern Canada, land cover, soil types, and hydrology have been mapped in detail (see Methods). The GIS approach directly predicts sites suitable for ground truthing (Wu and Smeins 2000; Aitken *et al.* 2007). Mann *et al.* (1999) used a similar approach to predict the location of rare, calcareous soil habitat. Although our GIS model was comparatively simple, it proved immediately useful by identifying potential new sites, with considerable accuracy, and thereby greatly increasing the efficiency of field surveys.

Moreover, GIS mapping of West River led to the discovery of a remarkably dense cluster of Orange-fruit Horse-gentian (over 140 plants) growing in mature, closed-canopy forest that would not have been considered habitat based on previous surveys. This forest stand was probably spared from historical logging because it grows on a steep slope. The discovery of many plants beneath a canopy of large White Ash, maple, and Red Oak along West River, and again in mature mixed forest along Rights River, suggests that young deciduous forest stands, such as those along most floodplains here, are not prime habitat for the species. The species may be encountered most often beneath suboptimum early second-growth forest (White Ash, Common Apple, cherry, young maple) because the preferred habitat—mature, late-successional forest—is so rare in northern Nova Scotia. Thus, horse-gentian may be rare at least partly because its habitat is rare. Creating similar habitat maps for other regional rivers would help in locating additional unknown patches of horse-gentian and determining whether lack of habitat limits the abundance of the species.

The frequency with which horse-gentian is found in the floodplains of Antigonish County may be explained by the relatively high pH there compared with upland sites. Hill and Garbary (2011) and Taylor and Tam (2012) found that the upland sites of Antigonish river valleys were significantly more acidic than the floodplains. Hill and Garbary (2011) also concluded that soil calcium is a determining factor in the presence of large-seeded herbs, including horse-gentian. Preference for high-calcium soils would align with the historical pattern of finding horse-gentian in limestone-rich areas elsewhere (Barton 1818; Ogle 1980; Laughlin and Uhl 2003; Mazerolle *et al.* 2018) and is consistent with the robust population of the species among the gypsum cliffs of Lower South River.

The PAM fluorometry confirms that Orange-fruit Horse-gentian is a shade-adapted plant that is stressed by exposure to full sunlight. However, the observation of apparent stress among floodplain plants along South River and unstressed functioning among upland plants nearby questions the conclusion that horse-gentian grows best in moist floodplains. Plants growing in Frasers Mills Upland also had the highest density of fruits per unit stem length among the sites compared. Taken together, these data suggest that South River floodplain provides less favourable habitat than other river floodplains or even some upland sites. The important difference appears to be the lower canopy cover (class 2, mostly open), and hence greater understorey light penetration, along South River compared with the other river valleys (class 3, mostly closed). Most flowers develop fruits, so pollination does not appear to be limiting. These observations support the contention that ideal habitat for horse-gentian is mature, closed-canopy forest with open understorey, and the association of the species with river valleys arises independently from a preference for calcium-rich soil.

This conclusion calls into question earlier suggestions that periodic disturbance is necessary to maintain habitat for Orange-fruit Horse-gentian (Ogle 1980; Laughlin and Uhl 2003). Taylor and Tam (2012), noting the association of horse-gentian with early successional trees in the river valleys and its absence in closed-canopy forest nearby, suggested that the plant may depend on disturbance to create and maintain habitat. However, it now appears more likely that mature forest, such as along West and Rights rivers, provides better habitat and disturbance is important only where it prevents growth of dense thickets of other plants. Then why does horse-gentian not occur in mature, hardwood forest farther upstream in the Pomquet/Black Avon and South River systems? It is possible that the species is rebounding from a historical decline due to land clearing and has yet to recolonize upstream habitat.

Seed dispersal in horse-gentian is probably by endozoochory, possibly dominated by White-tailed Deer. The fruits float, so dispersal by hydrochory cannot be ruled out. However, the presence of large patches of horse-gentian on one bank of South and West rivers, but not on the other, suggests that rivers may be acting as barriers, rather than vectors, to dispersal. Moreover, the upland sites at Frasers Mills and

St. Andrews were atop a steep incline from the floodplain and further separated by a long-extant gravel road. Therefore, the uphill slope was not a barrier to dispersal, nor was the road. The population scattered along upper Rights River was also far uphill from the river. These observations reinforce our hypothesis that horse-gentian is dispersed by means other than, or in addition to, hydrochory.

Additionally, horse-gentian stems with deer damage were recorded throughout the course of the study and along all four rivers, indicating that deer browsing is widespread. Damage from deer browsing was particularly evident along West River, which supports the largest horse-gentian population. We do not speculate on the reason for the apparent different browsing pressure among rivers and there appear to be no deer density data for the area. We have direct photographic evidence of a deer consuming a plant with fruits. We observed many genets of horse-gentian along deer trails.

Endozoochoric dispersal by deer also helps explain: (1) the association of horse-gentian with Common Apple along all three rivers (Figure 2), and (2) why some habitat that appears to be suitable for the species is not colonized. Deer readily feed on fallen apples and therefore spend time beneath apple trees. Horse-gentian seeds excreted in their faeces are likely to accumulate beneath apple trees. Of 30 horse-gentian plants recorded at Frasers Mills Upland, 18 grew near apple trees.

Female White-tailed Deer are strongly territorial (Beier and McCullough 1990), occupying home ranges of 20–140 ha from which they rarely stray (Beier and McCullough 1990; Storm *et al.* 2007; Walter *et al.* 2009). A doe with a territory encompassing a river valley is unlikely to cross into another valley. Horse-gentian dispersal by deer to more distant patches of new habitat would thus depend on occasional dispersal by young deer (Long *et al.* 2005) or migrations between summer and winter habitat (Messier and Barrette 1983). Deer are apparently responsible for dispersal of White Trillium (*Trillium grandiflorum* (Michaux) Salisbury) over distances of several hundred metres to 4 km; many herbs lacking obvious long-term dispersal mechanisms may be occasionally dispersed by deer (Vellend *et al.* 2003).

The browse selection of Snowshoe Hare often overlaps with that of White-tailed Deer (Telfer 1972), so both species may be consuming horse-gentian. Yet the hare's preference for woody shrubs (Turkington *et al.* 2002) and a lack of observed damage from hares (whose incisors clip stems cleanly, compared with rough breakage from deer) throughout our survey suggest it is unimportant compared with deer. Other possible mammalian dispersers (chipmunks, Raccoon, porcupines) were infrequently observed and have even smaller home ranges than White-tailed Deer (Forsyth and Smith 1973; Banfield 1974). We never observed birds feeding on the fruits. Therefore, endozoochory may impose a dispersal limitation (Eriksson and Ehrlén 1992), which impedes colonization of all available habitat. If a local population of horse-gentian is extirpated, as may have happened along lower Black Avon River, it may be many years before a deer travels far enough to bring in new seeds. Collection of seeds from deer faeces would be necessary to confirm this dispersal mechanism. Longevity of the seedbank is unknown.

The upper limit of dispersal by White-tailed Deer, specifically the distance a deer can travel on the maximum gut retention time, may exceed 10 km (Vellend *et al.* 2003). Dispersal limitation may explain the absence of horse-gentian from apparently suitable habitat along Tracadie River, which lies 15 km east of Pomquet/Black Avon River, but not from the floodplain of Brierly Brook, which lies between Rights and West rivers (Figure 1). No horse-gentian has been found along Brierly Brook despite extensive searches by Taylor and Tam (2012) and us. White-tailed Deer are common along the brook, even within Antigonish, so dispersal limitation is unlikely. The high electrical conductance (a measure of dissolved ion concentration) of Brierly Brook compared with other regional streams (B.R.T. unpubl. data) argues against calcium deficiency, and physical habitat in its floodplain is indistinguishable from floodplains along other rivers. The remaining possibility is that floodplain forest along this historically disturbed stream has only recently matured and a colonization event has not yet occurred.

Conclusions

It appears that both habitat limitation (Clark *et al.* 2007) and dispersal limitation (Eriksson and Ehrlén 1992) contribute to the rarity of Orange-fruit Horse-gentian in Antigonish County. Combined habitat and dispersal limitation is likely to apply to any rare plant species restricted to isolated patches of habitat embedded in an inhospitable landscape, such as often created by human disturbance. How readily new plants establish in a habitat patch may depend not only on the size and geographical isolation of that patch, but also on the efficacy of vectors carrying propagules from one patch to another. Both these factors may contribute to maintaining rarity of a species. Our study also highlights the difficulty of identifying best habitat for a species (here, probably mature hardwood forest) when good habitat is so rare that most plants occur in sub-optimal habitat (early successional forest). A GIS-based modelling approach continues to prove useful for directing field searches toward the most promising sites. Further work is needed to confirm whether Orange-fruit Horse-gentian can survive in what appears to be unoccupied habitat, such as along Brierly Brook, and whether White-tailed Deer is a key vector of seed dispersal. The implications for the species given expected future changes in land use, climate, and species abundances in Nova Scotia also remain to be explored.

Author Contributions

Writing – Original Draft: T.H.; Writing – Review & Editing: B.R.T.; Conceptualization: B.R.T.; Investigation: T.H., B.R.T., and D.J.G.; Methodology: B.R.T., D.J.G., and M.S.; Formal Analysis: B.R.T. and M.S.; Funding Acquisition: B.R.T.

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