The unreliable concept of native range as applied to the distribution of the rusty crayfish (*Faxonius rusticus*) in North America

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Abstract The concept of native range in invasion biology is difficult to define since, in many cases, this type of range is unknown and cannot be determined. We investigate the uncertainties related to this concept by focusing on the distribution of *Faxonius rusticus* (Girard, 1852), also known as the rusty crayfish, which is perceived as possibly the worst invasive crayfish species in North America. In this study, we undertake a comprehensive literature review, which includes 430 studies published between 1852 and 2018, in order to analyze the native and introduced ranges of this species. The rusty crayfish was reported to occur in 33 states in the U.S.A. and 3 Canadian Provinces. Ten of these U.S. states and one Canadian Province have been included multiple times in both the native and the non-native ranges of this crayfish. The confusion regarding the limits and history of the native range of the rusty crayfish has implications for the conservation of this species in various jurisdictions. This review also demonstrates that even for intensely studied species perceived as invasive, we often do not have a clear understanding of essential concepts such as native and non-native range.

Keywords Non-native • Invasive species • Invasion biology • Biogeography • Great Lakes region • Freshwater ecosystems

Introduction

The geographic distributions of species have been a major topic of interest for naturalists and biologists for centuries, as shown, for example, in the classic works of Alexander von Humboldt (1805) and Alfred Russel Wallace (1876). Charles Darwin dedicated two chapters of his seminal book *On the origin of species* (1859) to the geographical distribution of species, and mentioned interesting examples of long-distance dispersal, such as the transport of plant seeds and freshwater molluscs on the muddy feet of birds. Almost one century later, British ecologist Charles Elton published the book *The ecology of invasions by animals and plants* (1958), which is generally acknowledged as the starting point of the young field of invasion biology. The rise of invasion biology, however, did not start in earnest until decades later, in the early 1990s (Ricciardi & MacIsaac, 2008; Guiașu, 2016; Guiașu & Tindale, 2018).
As invasion biology started growing rapidly and becoming more influential in the last three decades or so, researchers in this field began to focus more and more on concepts such as native range, in order to determine the native or non-native status for an ever-expanding number of species (Guiasu, 2016). Despite this increased focus, leading invasion biologists agree that the concept of native range still lacks a formal theoretical definition in invasion biology (Courchamp et al., 2020; Pereyra, 2020). Identifying non-native species is based on the assumption that the native range is known or can be determined. Nevertheless, this is not the case in many instances (Guiasu, 2016; Orlova-Bienkowskaja & Volkovitsh, 2018; Pereyra, 2020). Thus, the task of differentiating native species from non-native species can prove to be rather difficult, or virtually impossible, in many cases since the limits and history of native ranges, as well as the diverse means of species’ dispersal, are often unknown (Guiasu, 2016; Essl et al., 2018; Guiasu & Tindale, 2018; Pereyra & Guiasu, 2020).

In his book about the dynamic nature of the distributions of species, Gaston (2003) stated that the study of the limits of the geographic ranges of species “should be a central objective of ecological research,” before discussing some of the challenges associated with the determination of such limits and the current general lack of a “comprehensive understanding of why any given species occurs where it does and not elsewhere.” The subjective nature of the native range concept was discussed in detail by Guiasu (2016) and Guiasu & Tindale (2018). Even more recently, a rather intense debate about the definition and usefulness of the native range concept in invasion biology was featured in the pages of the journal Conservation Biology (Courchamp et al., 2020; Pereyra, 2020; Pereyra & Guiasu, 2020). Pereyra & Guiasu (2020) argued that the concept of native range is not well defined, not universal, and therefore not useful in quite a few cases in conservation biology, and in invasion biology in particular.

Determining the limits and history of native ranges can be particularly challenging in situations where species expand their ranges by moving into adjacent areas which are not separated from the assumed previous ranges by any insurmountable geographic barriers. In such cases, we often have no way of knowing if the species expanded their ranges entirely on their own, without human assistance, or with the direct or indirect help of people. One such example is provided by Faxonius rusticus (Girard, 1852), also known as the rusty crayfish, in North America. This freshwater species has been expanding its North American range in the last several decades often by moving through interconnected rivers and lake systems (Guiasu, 2016; Guiasu & Tindale, 2018).

Even though the rusty crayfish is indeed unquestionably native to North America, this species is currently considered invasive in many regions of this continent, and the appearance of this crayfish at new locations is generally treated as an “invasion,” despite the frequent absence of sufficient historical biogeographic data and persuasive information about the means of dispersal (Guiasu, 2016). As a result of the “invasive” label often rather casually applied to this species, the rusty crayfish is the target of control programs that seek to eradicate it from certain lakes and streams (Hein et al., 2006, 2007). However, the exact extent of the native range and the means of dispersal of this crayfish species remain unclear at least in some regions (Guiasu, 2016).

In the current study, we analyze the distribution of the rusty crayfish (Faxonius rusticus) in North America by reviewing all the information we could find on this topic in the scientific literature, and discuss the uncertainties about the extent of the native and non-native ranges of this species. Our aim is to use this well-known and much studied species as a cautionary example of the potential problems with the native range concept.

Materials and methods

Literature search

In order to review the literature on the rusty crayfish, the following terms were used for a search on Google Scholar (last accessed on March 19, 2019): rusty crayfish; Orconectes rusticus (a previous name for this species used in the majority of the references cited in this study); Faxonius rusticus (a newer name assigned to the species in 2017); and Cambarus rusticus (the older name initially assigned to this species by Girard in 1852, before the change to the genus Orconectes). This comprehensive literature search yielded 430 publications, consisting mainly of peer-reviewed journal articles, as well as a few scientific books,
technical reports, and academic dissertations. Of these publications, 412 were accessed online through a York University subscription with Google Scholar, while *The Crayfishes of Ohio* (Turner, 1926) and the *Ecology of the Crayfish Orconectes rusticus in Northern Wisconsin* (Lorman, 1980) works were acquired physically through an interlibrary loan with Lakehead University. Sixteen other publications were accessed from Radu Guiaşu’s personal reprint and book collection (Huntsman, 1911; Hobbs, 1974; Smith, 1981; Hobbs & Jass, 1988; Maude, 1988; Momot et al., 1988; Jezerinac et al., 1995; Momot, 1996; Hamr, 1998; Holdich, 2002; Lieb et al., 2007; Hamr, 2010; Nadelhoffer et al., 2010; Rosenberg et al., 2010; Somers & Reid, 2010; Booy et al., 2015). Thirty-one other publications could not be accessed at all, either electronically or physically. These 31 publications were not included in the analysis. Given the extensive nature of the literature search, and the fact that we were able to access and analyze the information in 430 specialized publications, published between 1852 and 2018, we do not believe that the absence of the 31 studies we could not access would have a significant impact on the conclusions drawn from the examination of our vast data set.

Native and introduced range survey

In order to gather the information on the native or non-native range assignments for the rusty crayfish in various jurisdictions, and identify the potential discrepancies with regard to the native and introduced ranges for this species, all 430 accessible publications were read very carefully, and the relevant information was tabulated (Table 1 and Online Appendix A). Only clear and specific references to particular U.S. states or Canadian Provinces were included in the data set shown in Table 1. More ambiguous references, such as “Ohio River basin” or “Ohio River valley” were not included, because the Ohio River basin covers 14 states in the U.S.A., and therefore we found that such descriptions were too vague to allow us to assign the distribution to any particular state or states. On the other hand, reports such as “Ohio River at Cincinnati” were included among the data in Table 1, since the Cincinnati location is clearly found within the state of Ohio.

Information about the *F. rusticus* distribution was classified into three separate categories. The first two categories were composed of clearly defined native and introduced ranges, respectively, given in studies where authors explicitly mentioned the native and/or non-native status of the rusty crayfish in well-defined jurisdictions (U.S. states and Canadian Provinces). A third category was used in cases where rusty crayfish geographical data were presented without any specification as to whether the described regions were part of the species’ native range or introduced range. When the range in a particular category was not discussed at all in a study, this was indicated in the Appendix A table as well. This allowed us to understand the frequency with which various types of ranges were discussed in the scientific literature which focused, exclusively or partially, on the rusty crayfish. The 430 studies listed in Online Appendix A are arranged in chronological order, beginning in 1852 and ending in 2018.

For the purposes of our analysis, we have also divided the data set into two unequal time periods: 1) the period between 1852 (the year of the first study we found which mentioned this crayfish species) and 1989 (a period of 137 years); and 2) the 28-year-long period between 1990 (starting with the Bruski & Dunham, 1990 study) and 2018 (the last year included in our data set). While any such subdivision of the data set can be somewhat arbitrary, we chose the year 1990 as the first year of the second time period in our analysis, because there has been a dramatic rise in the number of publications in the young field of invasion biology since the early 1990s (Ricciardi & MacIsaac, 2008; Guiaşu, 2016; Guiaşu & Tindale, 2018). Since the rusty crayfish is considered to be an invasive species, we wanted to find out if there was an increased interest in this species, and its native or non-native ranges in particular, starting in the 1990s, as a result of the rise of invasion biology.

In general, crayfish behavioral and physiological studies, for example many of those from the labs of researchers such as David Dunham, Brian Hazlett, Robert Huber, Paul Moore, and Ann Jane Tierney, did not discuss species distributions and were not concerned with biogeographic concepts such as native or non-native ranges. However, when such studies involved the collection of rusty crayfish in a well-defined jurisdiction (such as Ohio, Michigan, or Ontario, for example), we included this information in our data set, usually in the unspecified range category (unless the native or non-native status of the rusty crayfish was clearly mentioned).
Recently, Crandall & De Grave (2017) assigned the surface water crayfish previously grouped in the genus *Orconectes* Cope 1872, including *Orconectes rusticus*, to the genus *Faxonius* Ortmann, 1905. Thus, all the *Faxonius* species mentioned in this study used to be placed in the genus *Orconectes* prior to the

### Table 1
Summary of the numbers of times various U.S. states and Canadian provinces were listed as part of the native, non-native, or general range (native or non-native not specified) of the rusty crayfish

| Geographic location (US state or Canadian province) | Total number of listings | Number of native range listings | Number of introduced listings | Number of range listings (native or non-native not specified) |
|-----------------------------------------------------|--------------------------|---------------------------------|------------------------------|------------------------------------------------------------|
| United States                                       |                          |                                 |                              |                                                            |
| Ohio                                                | 169                      | 62                              | 11                           | 96                                                         |
| Wisconsin                                           | 123                      | 1                               | 108                          | 14                                                         |
| Indiana                                             | 74                       | 55                              | –                            | 19                                                         |
| Kentucky                                            | 74                       | 55                              | –                            | 19                                                         |
| Michigan                                            | 70                       | 24                              | 27                           | 19                                                         |
| Illinois                                            | 51                       | 15                              | 23                           | 13                                                         |
| Tennessee                                           | 43                       | 17                              | 11                           | 15                                                         |
| Iowa                                                | 26                       | 2                               | 11                           | 13                                                         |
| Minnesota                                           | 24                       | 1                               | 21                           | 2                                                          |
| Pennsylvania                                        | 23                       | –                               | 13                           | 10                                                         |
| New Mexico                                          | 19                       | –                               | 18                           | 1                                                          |
| Missouri                                            | 17                       | 3                               | 2                            | 12                                                         |
| New York                                            | 17                       | –                               | 9                            | 8                                                          |
| Massachusetts                                       | 14                       | –                               | 12                           | 2                                                          |
| West Virginia                                       | 13                       | 2                               | 11                           | –                                                          |
| Maine                                               | 12                       | –                               | 12                           | –                                                          |
| New Hampshire                                       | 8                        | –                               | 8                            | –                                                          |
| Vermont                                             | 8                        | –                               | 8                            | –                                                          |
| Connecticut                                         | 7                        | –                               | 7                            | –                                                          |
| North Carolina                                      | 5                        | –                               | 5                            | –                                                          |
| Texas                                               | 5                        | –                               | –                            | 5                                                          |
| New Jersey                                          | 4                        | –                               | 3                            | 1                                                          |
| Oregon                                              | 4                        | –                               | 4                            | –                                                          |
| Alabama                                             | 3                        | 2                               | –                            | 1                                                          |
| Arkansas                                            | 3                        | –                               | –                            | 3                                                          |
| Kansas                                              | 3                        | –                               | –                            | 3                                                          |
| Virginia                                            | 3                        | 2                               | 1                            | –                                                          |
| Utah                                                | 2                        | –                               | 2                            | –                                                          |
| Colorado                                            | 1                        | –                               | 1                            | –                                                          |
| Mississippi                                         | 1                        | 1                               | –                            | –                                                          |
| Nebraska                                            | 1                        | –                               | 1                            | –                                                          |
| Washington                                          | 1                        | –                               | 1                            | –                                                          |
| Wyoming                                             | 1                        | –                               | 1                            | –                                                          |
| Canada                                              |                          |                                 |                              |                                                            |
| Ontario                                             | 94                       | 10                              | 66                           | 18                                                         |
| Quebec                                              | 6                        | –                               | 6                            | –                                                          |
| Manitoba                                            | 4                        | –                               | 4                            | –                                                          |

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publication of the Crandall & De Grave (2017) study. We follow this updated classification, and use the new *Faxonius rusticus* (Girard, 1852) scientific species name for the rusty crayfish in this study.

**Results**

The comprehensive literature review included 430 studies published between 1852 and 2018—a span of 166 years (Online Appendix A). We compared the two time periods—the one between 1852 and 1989 and the one between 1990 and 2018—to determine the possible effect of invasion biology on the number of studies published. Overall, 139 studies mentioning the rusty crayfish were published between 1852 and 1989. Thus, during this period, which covers 137 years, an average of 1.01 studies per year which referred to the rusty crayfish were published. However, during the subsequent 28 years, between 1990 and 2018, 291 studies mentioning the rusty crayfish were published, and, therefore, an average of 10.39 such studies per year were published during this much shorter period. Thus, the number of studies published per year increased more than tenfold between 1990 and 2018, in comparison to the period covering the previous 137 years.

When we analyzed the numbers of times, particular range types (native, non-native, or unspecified) were not discussed in the studies included in our data set (Appendix A), we obtained the following numbers: 742 “not discussed” entries for the entire data set (1852–2018); 268 (or 36.12% of the total) “not discussed” entries for the 1852–1989 period; and 474 (or 63.88% of the total) “not discussed” entries for the 1990–2018 period.

Looking at the data in more detail, we found that the 268 “not discussed” entries for the 1852–1989 period were subdivided in the following way: native range was not discussed in 113 studies, non-native range was not discussed in 97 studies, and the unspecified range (range not clearly identified as either native or non-native) was not discussed in 58 studies. During the 1852–1989 period, all three types of ranges were not discussed at all in 18 (12.95%) of the 139 studies. So, less than 13% of the studies published during this period failed to mention the geographic range of the rusty crayfish altogether. During this same period (1852–1989), neither native nor non-native ranges were mentioned in 97 studies (or 69.78% of the total number of 139 studies for this period). If we subtract the number of studies (18) where range was not mentioned at all, we are left with 79 studies (or 56.83% of the total) in which range was mentioned but not identified as either native or non-native. This means that in more than one half of the studies published during this 137-year period, no distinction was made between native and non-native ranges. The data also show that between 1852 and 1989, the non-native range was mentioned in 16 more studies than the native range. On the other hand, there were no studies published between 1852 and 1989 in which the native range was mentioned without the non-native range. So, the native range was never mentioned alone in any of these studies, without the non-native range being discussed as well.

The 474 “not discussed” range entries recorded during the 1990–2018 period were subdivided in the following way: native range was not discussed in 158 studies; non-native range was not discussed in 104 studies; and the unspecified range (native or non-native range not clearly identified) was not discussed in 212 studies.

During the 1990–2018 period, none of the three types of ranges were discussed at all in 25 (or 8.59%) of the 291 studies published. During this same period, neither native nor non-native ranges were mentioned together in 97 (or 33.33%) of the total 291 studies published. If we subtract the 25 studies during which the range was not mentioned at all, we are left with 72 studies (or 24.74% of the total) in which range was mentioned but not identified as either native or non-native. So, in about one-quarter of the studies published between 1990 and 2018, the range was mentioned, but no distinction was made between native and non-native ranges. Clearly, the percentage of studies in which range was mentioned but not clearly identified as either native or non-native decreased substantially over time, from almost 57% during the 1852–1989 period to less than 25% between 1990 and 2018. Thus, after 1990, a much higher percentage of studies than before identified range as either native or non-native.

During the 1990–2018 period, the non-native range was mentioned alone (without the native range also being mentioned) in 61 studies, whereas the native range was mentioned alone (without the non-native range also being mentioned) in only 7 studies.
Therefore, between 1990 and 2018, non-native range was mentioned without the native range in almost nine times more studies than the other way around. This suggests a predominant focus on the non-native, or introduced, range of the rusty crayfish in quite a few studies.

For the entire period included in our study (1852–2018), non-native range was mentioned alone (without the native range being also mentioned) in 77 studies, whereas the native range was mentioned alone (without the non-native range also being mentioned) in only 7 studies.

The data showing the numbers of states in the U.S.A. and Canadian Provinces where *F. rusticus* was listed as either native, or non-native, or both, are shown in Table 1. According to the data summarized in Table 1, *F. rusticus* was reported at least once from 33 states in the U.S.A. and 3 Canadian Provinces. Ten states in the U.S.A. and one Canadian Province (Ontario), representing about one third of the United States and Canadian jurisdictions included in the analysis, respectively, had both native and non-native listings reported for the rusty crayfish. Of the 20 U.S. states where only one range type (native or non-native) was listed, 2 were listed only in the native range category, 2 were listed in the native range and unspecified range-type categories, 11 were listed only in the non-native (or introduced) range category, and 5 were listed in the non-native range and unspecified range-type categories. The remaining 3 U.S. states were listed only in the unspecified (native or non-native status unclear) category (Table 1). The two Canadian Provinces (Manitoba and Quebec) for which only one type of range was given only had non-native range listings for *F. rusticus*.

**Discussion**

*Faxonius rusticus* currently has a wide range in North America and the presence of this species was reported in 33 U.S. states and 3 Canadian Provinces (Table 1). Of course, as one of us (Guiaşu, 2016) has pointed out before, the borders of states and provinces are simply lines on a map, drawn for political reasons, which have no significance for any other species than our own. These artificial borders generally have no ecological meaning and most often do not separate distinct ecosystems. Nevertheless, since the vast majority of the studies we analyzed refer to the distribution of crayfish in various states and provinces, and since these regions are clearly defined on maps, we are also using U.S. states and Canadian Provinces as indicators of where the rusty crayfish may be found and how the range of this species may have changed over time.

The prevalent current expert opinion seems to be that the rusty crayfish is native to the Ohio River basin and the midwestern areas of the U.S.A., although the exact history, extent, and limits of this native range remain unclear (Dresser & Swanson, 2013; Guiaşu, 2016). There are many disagreements in the scientific literature about some of the regions which may, or may not, be part of the native range of this crayfish species. These disagreements have conservation implications. Most of these disagreements focus on the 10 U.S. states (Ohio, Wisconsin, Michigan, Illinois, Tennessee, Iowa, Minnesota, Missouri, West Virginia, and Virginia) and the one Canadian Province (Ontario) which have been included, in various studies, in the native range and the non-native range of *F. rusticus*. In certain studies, some of these states were included in both of those ranges at the same time (for example: Taylor, 2000). Among these 10 U.S. states, there are only 4 (Ohio, Michigan, Illinois, and Tennessee) for which we have double digit numbers of entries in both the native range and the non-native range columns (Table 1). Therefore, we would expect most of the controversies and disagreements regarding the type of range (native or non-native) assigned to the rusty crayfish to be related to these particular 4 states, and, as a result, we will analyze the information regarding these 4 states first and in more detail.

**Ohio**

As can be seen in Table 1, Ohio was listed as part of the native range of the rusty crayfish much more often than in the non-native range category (62 to 11 studies, respectively), although a majority of studies (96) mentioning Ohio, including the first 19 listings for this state in Appendix A, did not specify whether *F. rusticus* was native or non-native there. Rhoades (1944a) was the first to include Ohio specifically into the native range of the rusty crayfish. The second study which assigned Ohio to the native range of this species was the one by Crocker & Barr (1968). Although Rhoades (1944a) also seemed to place Ohio within the non-native range of *F. rusticus*, this information was
somewhat ambiguous. The first unambiguous inclusion of Ohio into the non-native range of the rusty crayfish was found in a study by Jezerinac (1982), which was published 130 years after the work by Girard (1852) where some information about the distribution of this species was first mentioned. More confusingly, perhaps, in some studies, certain regions of Ohio were declared as being part of the native range of the rusty crayfish, while other regions of this state were considered parts of the non-native range. These regional range assignments were sometimes different in various studies. For example, Butler & Stein (1985) regarded *F. rusticus* as native in western Ohio, but invasive in east-central and southern Ohio. Rahel (1988) and Jezerinac (1991) considered eastern Ohio as part of the non-native range of *F. rusticus*. However, Tierney & Dunham (1984) declared the rusty crayfish native to eastern Ohio, and Lorman (1975) thought that this crayfish species was native to northeastern Ohio. The southwestern, or southwest, Ohio region was listed specifically as part of the *F. rusticus* range in 9 studies. Seven of these studies (Perry et al., 2001, 2002a, b; Dubé & Desroches, 2007; Davis et al., 2012; Roth et al., 2012; and Peters & Lodge, 2013) included southwestern Ohio in the native range of the rusty crayfish, but St. John (1991) disagreed, and assigned this same part of Ohio to the non-native range, while Claussen et al. (2000) did not specify whether southwestern Ohio belonged to the native or the non-native range.

**Michigan**

In this state, the rusty crayfish is listed as native in 24 studies and non-native in 27 studies, while the type of range (native or non-native) is not specified in 19 studies. The first 9 listings referring to Michigan in Appendix A do not specify the type of range (native or non-native) this state belongs to. Crocker & Barr (1968) were the first to assign Michigan to a specific type of range, and these authors found the rusty crayfish to be native in this state. The study by Charlebois (1994) was the first to include Michigan in the non-native range of *F. rusticus*, and Momot (1996) and Lodge et al. (1998) followed suit. In fact, after the mid-1990s, it seems that including Michigan in the non-native range for this crayfish species became the dominant position, and this coincided with the rise of invasion biology. Taylor (2000) found that the rusty crayfish was native to southeastern Michigan but non-native in the rest of that state. Three other studies (Lorman, 1975; Capelli, 1982; and Capelli & Magnuson, 1983) specifically found the rusty crayfish to be native to southern Michigan, while DiStefano et al. (2009) were even more specific, and thought that *F. rusticus* was native to the “southeastern corner of Michigan.” On the other hand, Keller & Hazlett (2010) found that the rusty crayfish was non-native to “northern and lower Michigan.”

**Illinois**

This is another state which has been included several times in both the native and the non-native range categories for the rusty crayfish—15 times in the native range column and 23 times in the non-native range column, respectively, as well as 13 times in the unspecified range type column (Table 1). The first 10 listings for this state in Appendix A do not specify the type of range (native or non-native) it is assigned to. The first specific type of range is given by Hobbs (1972), and this author considered the rusty crayfish to be a native species in Illinois. The first study to include Illinois in the non-native range of *F. rusticus* was the one by Page (1985). Taylor (2000) considered the rusty crayfish to be native to southwestern Illinois and non-native in the rest of the state. It could be argued that this crayfish may be native to a part or parts of Illinois and non-native in the rest of the state. However, the study by Taylor (2000) is the only one which places Illinois in both the native and the non-native range categories. All other studies listed in Appendix A which mention Illinois place this state either in the native range category or in the non-native range category.

**Tennessee**

This state has been included 17 times in the native range and 11 times in the non-native range of the rusty crayfish. There were also 15 listings in the unspecified range-type column, including the first 12 entries for this state in Appendix A. The first specific type of range is given by Hobbs (1974), who considered the rusty crayfish to be native to Tennessee. Crocker & Barr (1968) agreed with this assessment by Hobbs (1974), but Hamr (1998) and Lodge et al. (2000a) disagreed and included Tennessee in the non-native range category.
range of *F. rusticus*. David Lodge and researchers working in his lab were very influential in getting the rusty crayfish recognized as an invasive species and spreading this notion in the specialized literature, based mainly on studies conducted in some northern Wisconsin lakes (for example, Olsen et al., 1991; DiDonato & Lodge, 1993; Kershner & Lodge, 1995; Hill & Lodge, 1999).

The situation in Wisconsin seems somewhat more clear, since the vast majority of listings for this state (108) are in the non-native range column. The high number of studies in this category reflects, at least in part, the high level of research interest in the rusty crayfish as an invasive species in Wisconsin. However, there was also one listing for this state in the native range column, and 14 listings did not specify the type of range (Table 1). The first seven entries for this state in Appendix A did not specify the type of range (native or non-native). The first specific type of range was given by Capelli (1975), who included Wisconsin in the non-native range of the rusty crayfish. This was followed by Lorman (1975) who cited Capelli (1975), but listed Wisconsin as a part of both the non-native and the native range of *F. rusticus*.

The other five states (Iowa, Minnesota, Missouri, West Virginia, and Virginia) which appear in both the native and the non-native range columns have comparatively low numbers of listings overall. Iowa, Minnesota, and West Virginia are more often considered to be part of the non-native range of the rusty crayfish, whereas Missouri and Virginia appear slightly more often in the native range column than in the non-native range one (Table 1). To complicate matters further, Wetzel et al. (2004) conducted field work and examined relevant museum specimens and determined that at least some records from Iowa and Minnesota previously attributed to *F. rusticus* actually belong to the similar species *Faxonius luteus* (Creaser, 1933), which is regarded as a native species in these two states. Based on these observations, Wetzel et al. (2004) suggested that the ranges of both *F. rusticus* and *F. luteus* should be reassessed, not only in Iowa and Minnesota, but also perhaps in parts of Wisconsin and Illinois, where some *F. luteus* specimens may have been mistakenly identified as *F. rusticus*.

Twenty of the remaining 23 U.S. states listed in Table 1 appear either in the native range column or in the non-native range column, but never in both of these columns. Two of these states (Indiana and Kentucky) have plenty of listings in the native range column (55, for each of these two states), and some listings in the unspecified type of range column (19 in each case), and can therefore be reliably included in the native range of the rusty crayfish based on current knowledge. The same pattern applies to Alabama, although there are few listings for this state (2 in the native range column and 1 in the unspecified type of range column). There was only one listing for Mississippi, which has been included as part of the native range of the rusty crayfish by Crocker & Barr (1968). However, since this is the only record from Mississippi in our data set, and given the fact that Crocker & Barr (1968) focused on the crayfish of Ontario, and referred to several subspecies of *F. rusticus* in their analysis, caution should be exercised in interpreting this listing. It is quite possible that the lone record of this species for Mississippi may in fact be reassessed and attributed to another similar and closely related crayfish species.

Species identification can be challenging for crayfish species, and mistakes can often be made (Guıaşçu, 2016). Taylor (2000) assigned *F. rusticus* to the *Faxonius juvenilis* (Hagen, 1870) species complex, which contains several closely related and very similar-looking species. The exact composition of this species complex was debated for more than 100 years, and, at various times, several species within this complex—such as, for example, *F. juvenilis*—were considered synonymous with *F. rusticus*. Since the differences between these species are very subtle, and all these species occupy similar habitats, it is often difficult to tell these species apart, and this creates additional problems for the assessment of their distributions.

Sixteen states (Pennsylvania, New Mexico, New York, Massachusetts, Maine, New Hampshire, Vermont, Connecticut, North Carolina, New Jersey, Oregon, Utah, Colorado, Nebraska, Washington, and Wyoming) never appear in the native range column for the rusty crayfish, and are listed only in the non-native range column or in both the non-native range and the unspecified type of range columns. As can be seen, these states are generally found in the northeastern and western areas of the U.S.A., often relatively far away from the presumed midwestern center of origin for this crayfish species. Therefore, at least some of these 16 U.S. states—for example those, such as New Mexico or Washington, not adjacent to regions where the rusty
crayfish is considered to be native—can probably be safely assumed to be part of the non-native range of *F. rusticus*.

For the remaining 3 U.S. states (Texas, Arkansas, and Kansas) listed in Table 1, we have relatively few distribution records for the rusty crayfish and none of these records specify the type of range. These records were also published long ago, either in the late nineteenth century or early in the twentieth century, before a clear focus on native and non-native ranges became fashionable. For example, the 5 records for Texas were published in 1884, 1885, 1886, 1889, and 1912, respectively, the 3 records for Arkansas were published in 1885, 1898, and 1912, respectively, and the 3 records for Kansas were published in 1890, 1912, and 1931, respectively. Given that the presence of *F. rusticus* has never been reported in these states since then, it is possible that these early records may have been erroneous due to the misidentification of the crayfish species. It is also theoretically possible that the rusty crayfish may have been present in these 3 states many decades ago, but disappeared from these locations since then.

Ontario is the only Canadian Province included in both the native range and the non-native range of *F. rusticus*. This province is listed 10 times in the native range column, 66 times in the non-native range column, and 18 times in the unspecified range-type column (Table 1). In their detailed book on the crayfishes of Ontario, which remains the most influential work of its type in the field for this region, Crocker & Barr (1968) were the first to include this province into a specific (native or non-native) type of range. These authors regarded the rusty crayfish as non-native in Ontario. The book by Crocker & Barr (1968) was important in establishing the notion that the rusty crayfish was non-native in Ontario. However, Hobbs (1972) disagreed, and was the first to refer to *F. rusticus* as a native species in Ontario. Jezerinac et al. (1995) thought that the rusty crayfish was native to southern Ontario, but non-native in northwest Ontario. The other two Canadian Provinces where *F. rusticus* was found—Manitoba and Quebec—were only included in the non-native range for this species.

Overall, 26 U.S. states and 3 Canadian Provinces were included in the non-native range of the rusty crayfish, and 14 U.S. states and 1 Canadian province were included in the native range of this species. The reported non-native range for this species is considerably larger than its native range (Table 1).

Interestingly, the first 32 studies mentioning the rusty crayfish, which are listed in Appendix A and were published between 1852 and 1942 (during a period of 90 years), did not refer specifically to either native or non-native ranges. Thirty-one of these early studies offered information on the rusty crayfish range without specifying whether this range was native or non-native, and the remaining study did not discuss range at all. The first study listed in Appendix A which mentioned native and non-native ranges for *F. rusticus* was the one by Rhoades (1944a). Then, the next 20 studies in Appendix A did not discuss specifically either the native or the non-native range. The next work to refer to the native and non-native ranges of the rusty crayfish was the previously discussed book by Crocker & Barr (1968). Therefore, during the 116 years between 1852 and 1968, only two studies referred specifically to native and non-native ranges for this crayfish species. This suggests that concepts such as native and non-native range were not considered nearly as important during the second half of the nineteenth century and the first half of the twentieth century as they are today. With the rise of invasion biology, particularly in the last 30 years or so, reports about the distributions of species tended to focus more and more on whether these distributions were perceived as “native” or not. As a result, the percentage of studies which mentioned the rusty crayfish range without identifying this range as either native or non-native, out of the total number of studies listing the distribution of this species, declined from nearly 57% for the 1852–1989 period to less than 25% for the 1990–2018 period.

As shown in the previous section, the average number of studies per year which mentioned the rusty crayfish increased tenfold during the 1990–2018 period, in comparison to the 1852–1989 period. This dramatic increase may be attributed, at least in part, to the rise of invasion biology, which led to an enhanced focus on species perceived as invasive, such as *F. rusticus*. The data also showed that many more studies on the rusty crayfish mentioned the non-native range rather than the native range of this species, particularly since 1990, which suggests more of an emphasis on the non-native range, in keeping with an increased interest in the rusty crayfish because of its perceived invasive status in many areas.
In order for a species to be regarded as non-native, or even possibly invasive, the assumption is that the species expanded its range and reached new areas with human assistance. The fundamental problem with this assumption is that in many cases we simply do not know how various species, including *F. rusticus*, expanded their respective ranges. It is frequently assumed, for example, that the rusty crayfish was brought to various regions by fishermen who used this species as bait (Lodge, 1993a; Gunderson, 1995; Taylor, 2000; Marsden & Hauser, 2009). While this is certainly possible, no evidence is usually provided for such claims. In fact, Gunderson (1995) acknowledges that “there is no direct evidence” for the assertion that “anglers using crayfish as bait are thought to be the primary cause” for the spread of rusty crayfish in certain areas. Helgen (1990) stated that “There is no real information on human-caused dispersal of *F. rusticus* in Minnesota. Fishermen using crayfish as live bait have been implicated, but there is no data either on the extent of use of crayfish in northern and north central Minnesota (most fishermen use leeches and minnows), nor on the species of crayfish sold by live bait dealers in the state.”

Hamr (2010) mentions that *F. rusticus* “is thought to have been introduced into Ontario in the early 1960s, presumably by anglers from Ohio.” In other words, we do not really know how the rusty crayfish reached Ontario, but we assume, without evidence, that the Ohio fishermen must have brought these crayfish here about 60 years ago. This mere assumption validates potential and actual control programs against *F. rusticus*. In the same study, Hamr (2010) mentions various ways of managing this supposedly introduced crayfish species, including the eradication of new populations. Clearly, eradication would not be considered if the rusty crayfish would be regarded as a native species in Ontario.

*F. rusticus* is a resourceful crayfish species which can survive in a variety of freshwater aquatic habitats, including small ponds, large lakes, and various types of streams, and even, occasionally, in areas with mainly wet mud and little available surface water (Guiașu & Guiașu, 2003; Guiașu, 2007, 2008, 2016, 2021). The rusty crayfish is also able to dig fairly deep and extensive burrows in the banks of streams with clay substrate (Hamr, 1998). This species can dig burrows both in the field and in the lab, and has been observed to burrow in a variety of locations, for example in Ohio and Kentucky (Berrill & Chenoweth, 1982).

This is a crayfish species that is perfectly capable of dispersing itself efficiently without human help (Guiașu, 2007, 2008, 2016). Fitzpatrick (1987) stated that “man has helped *O. (P.) rusticus* in its invasions, but much of the range represents its own vigorous and successful expansion into areas breaking free of ice cover.” In other words, following the end of the last Ice Age, the expansion of the range of this species in North America was mostly achieved by natural means, and we should not punish *F. rusticus* for being good at dispersing itself while also occasionally taking advantage, as other species do as well, of certain human-made changes to the environment. There is no reason to believe that the post-glaciation northern expansion of the ranges of a variety of species, including crayfish, on the North American continent should not continue (Guiașu et al., 1996; Guiașu, 2016). Fitzpatrick (1987) also concluded that the exact ways in which *F. rusticus* may have expanded its range “will probably always remain unknown.”

The rusty crayfish is generally considered to be a non-native, and even invasive, species in the Great Lakes of North America region, and is usually discriminated against in this region as a result (Lodge et al., 2000; Olden et al., 2006; Olden et al., 2009; Johnson et al., 2009; Larson et al., 2017; Crossman et al., 2018; Cole et al., 2018, and many others). However, it is worth noting that this crayfish species is also regarded by many researchers as native to some states—such as Indiana, Ohio, Michigan, and Illinois—which border the Great Lakes (Table 1 and Appendix A). While referring to the rusty crayfish as “a nasty invader,” Gunderson (1995) acknowledges that this species “is native to parts of some Great Lakes states.” It is certainly possible to entertain the notion that *F. rusticus* may use its adaptability to various types of habitats and its superior dispersal abilities to expand its range gradually, and entirely on its own, through a network of interconnected rivers and tributaries all the way to the Great Lakes, and then within the vast Great Lakes freshwater system (Guiașu, 2016). Peters et al. (2014) stated that the rusty crayfish was present in Lake Erie for more than a century, and may have been “originally native to southwestern Lake Erie.” If that is indeed the case, then there would be nothing to prevent *F. rusticus* from expanding its range into the other Great Lakes,
and some of the streams and lakes adjacent to the Great Lakes (Guias¸u, 2016). Despite this, and the fact that the first record of the rusty crayfish from Lake Erie was from 1897, Peters et al. (2014) still label F. rusticus as a non-native species in all of the Great Lakes. This raises another question. For how long does a species have to be present at a certain location before we can finally accept it as a “natural” part of local ecosystems and leave it alone? Is a period of 123 years—the minimum length of time spent by the rusty crayfish in Lake Erie (as far as we know)—enough? These are the types of important questions invasion biologists generally do not seem particularly concerned about (Guias¸u, 2016). Jernelöv (2017) reviewed this topic in a recent book and found that “in most countries, there is no official policy with regard to the length of time a species has to be present before it more or less automatically receives citizenship or is considered native” and “where policies exist, they can differ significantly.” For example, according to Jernelöv (2017), federal law in Germany gives native status to any animal or plant species that can survive in the wild without human help for several generations, regardless of whether that species has been initially introduced by humans or not. However, in several other countries, species suspected of having arrived with human assistance are not officially accepted as native, or a natural part of local ecosystems, even after several decades or centuries. For instance, the common carp (Cyprinus carpio Linnaeus, 1758)—a well-known freshwater fish considered native to parts of Europe and Asia—is still regarded as an invasive species in Britain, even though it was introduced there before 1496 (Booy et al., 2015). This species is a valuable food fish, which was also successfully introduced into the U.S.A. in 1877 by the U.S. Fish Commission. Despite the fact that the common carp has been present in North America for 143 years, this fish is still not accepted by many as a truly local species on this continent (Guias¸u, 2016).

However, unlike the common carp, and other freshwater species which have been brought to North America from Europe and Asia by people, the rusty crayfish has originated and continued to evolve on the North American continent. Huston (1994) defined invaders as “species that have spread far beyond their original distribution, to distant continents or sometimes around the entire globe.” This definition does not seem to apply to the spread of the rusty crayfish in North America, at least in those regions adjacent to the presumed original, and poorly known, native range of this species. F. rusticus is accused of displacing the congeners Faxonius propinquus (Girard, 1852) and Faxonius virilis (Hagen, 1870) in some regions of North America—notably in Wisconsin and Ontario (Lodge, 1993a; Hamr, 1998). However, these three crayfish species are ecologically similar and have similar life cycles, diets, and habitat preferences (Lodge, 1993a). Furthermore, all three crayfish species are native to North America, where they remain quite common and very widely distributed, and they have broadly overlapping “natural” ranges. Thus, it would be hard to make the case that F. rusticus had a very different evolutionary history than these other closely related North American crayfish species. Lodge (1993a) reviewed the changing distributions and population dynamics of these three species in some northern Wisconsin lakes during the twentieth century, and noted that F. virilis was the most abundant crayfish in that region in 1930, but was then partially displaced by F. propinquus, which likely arrived in the 1950s, and then by F. rusticus, which reached the area probably in the 1960s and is capable of displacing the other two congeners in these lakes. Lodge (1993a) refers to the arrivals of both F. propinquus and F. rusticus in northern Wisconsin as “invasions from the southern Midwest” of the U.S.A., but these types of distribution and species composition changes can also be regarded as normal and should be expected over time. Newly arrived crayfish species may establish themselves successfully in certain regions mainly because they are better adapted to the changing local environmental conditions (Guias¸u, 2009). Interestingly, both F. virilis and F. propinquus are also perceived as “invasive” species when they expand their presumed native ranges further, to other regions of North America. For example, F. propinquus is considered native to southern and eastern Wisconsin but invasive in the northern part of that state, and the western range expansion of F. virilis in North America is also labeled as an “invasion” (Olden et al., 2006; Phillips et al., 2009).

The distributions of species are, of course, dynamic, and we cannot expect species to remain forever within the boundaries of the ranges we rather arbitrarily designated as “native” on their behalf (Guias¸u, 2016). There must have been many changes in the distributions of crayfish species in eastern and central North
America since the end of the last Ice Age, approximately 10,000 years ago, and we can expect more of these changes in the future as well, of course. Trying to stop or minimize potential range expansions by some of these crayfish species on their native continent, especially in areas adjacent to their presumed native ranges, and in the absence of clear information about means of dispersal, seems to be a rather dubious and largely futile exercise. Such attempts to control crayfish species perceived as “invasive” may also have unintended consequences and negative effects on other species (Guiasu, 2016). For example, chemicals which kill the rusty crayfish will also inevitably kill other crayfish species as well, including presumably native species (Gunderson, 1995; Olden et al., 2006). Also, given the previously discussed similarities among closely related crayfish species in North America, and the fact that even experts often have a tough time telling such species apart, enlisting the help of the public to remove rusty crayfish from various surface waters would probably lead to the destruction of several other crayfish species as well in the targeted areas. There are probably better ways to spend the limited conservation-related resources available (Guiasu, 2016; Guiasu & Tindale, 2018).

It should also be mentioned that sometimes changes in environmental conditions can lead to major declines in populations of both native and non-native crayfish species, including F. rusticus. For example, Edwards et al. (2009) found significant and geographically widespread population declines for all the seven crayfish species (native and non-native) sampled during a major survey of 100 lakes from a large region of south-central Ontario. This major decline occurred since the early 1990s and led to less diverse crayfish species assemblages in these lakes and much reduced or lost populations of all crayfish species in this region, including F. propinquus and F. virilis, which are considered native in Ontario, and the supposedly invasive F. rusticus. The rusty crayfish was rare in this region, and local populations of this species declined by 91% during this period of time. Overall, Edwards et al. (2009) stated that they “found no evidence to indicate that the presence of non-native crayfish was related to the decline of native species” and concluded that F. rusticus “was not a factor in the declines” of all these crayfish species in Ontario.

Our knowledge of historical North American crayfish distributions is often based on relatively few museum specimens, the oldest of which were usually collected in the late nineteenth century or the early twentieth century. For example, the oldest crayfish museum records in Ontario are from the early 1900s and are very incomplete. As a result, almost nothing is known about the distributions of crayfish species in this Canadian Province before the early twentieth century, and the relatively few records collected since then are not sufficient to give us a comprehensive picture of how or why these distributions may have changed over time (Guiasu, 2016, 2021; Pereyra & Guiasu, 2020).

Even assuming that F. rusticus may have made it to the Great Lakes with the aid of people back in the nineteenth century, or even earlier, it certainly seems like a long time has gone by since this crayfish species has lived in and around at least some of the Great Lakes, and there have been many irreversible changes to the habitats and species compositions of this vast region during all this time.

It is also entirely possible—indeed, likely—that the rusty crayfish may disperse itself both with and without human assistance, and, in any event, it is very difficult to differentiate naturally dispersing populations of such species from conspecific populations which benefit from direct or indirect human activities (Guiasu, 2016; Pereyra & Guiasu, 2020). Even in an article focused mainly on the invasion history of F. rusticus in Wisconsin, Olden et al. (2006) had to admit that “natural inter-lake dispersal of rusty crayfish is also possible and may represent an important vector of introduction” in that state. The problem is that, once a species such as the rusty crayfish is declared to be non-native, and especially invasive, in particular regions, this species is always likely to be viewed negatively by local conservation biologists and managers even in the absence of conclusive evidence for its non-native status, and even if the species may well be able to reach these regions by a variety of means, including “natural” (or nothuman assisted) ones. So, for example, although the rusty crayfish can probably reach Ontario on its own from nearby regions—such as Michigan and Ohio—where it is considered by many to be native, and may have already done this several times since the last Ice Age, this species is likely to be always considered invasive in this Canadian Province, simply because of the assumption that it may have been once brought here by people (Guiasu, 2016).
The debates about the exact extent of the native range of *F. rusticus* continue. For example, in a fairly recent study, Dresser & Swanson (2013) presented two alternative possible native ranges for this crayfish species. According to the first version, attributed to the researchers of The United States Geological Survey, the rusty crayfish is native to Indiana, Illinois, Kentucky, Ohio, and Tennessee. However, the other native range given in this same study for *F. rusticus* encompasses Ohio, Kentucky, Indiana, and Michigan. According to Dresser & Swanson (2013), this second native range is “accepted by researchers of invasive crayfish.” Based on what we know from the investigation of the relevant literature, this statement seems overly general, vague, and quite optimistic. Perhaps some researchers in this field may agree on this rather limited version of the native range of the rusty crayfish, but certainly not all. In support of the statement that researchers of invasive crayfish accept this particular version of the native range, Dresser & Swanson (2013) cite three studies: Taylor, 2000; DiStefano et al., 2009; and Peters & Lodge, 2009. As it turns out, however, none of these studies deal primarily with this revised version of the rusty crayfish’s range. Furthermore, in one of these studies, Taylor (2000) mentions “a less than clear understanding” of the ranges of several crayfish species, including *F. rusticus*, and admits that few specimens of this species from outside Kentucky were looked at, and the range of the rusty crayfish in states adjacent to Kentucky “is far from being completely known.” While, as previously discussed, it seems fairly safe to include Indiana and Kentucky within the native range of *F. rusticus*, and the Dresser & Swanson (2013) article appears to confirm that, many controversies about the exact status of this species in several other U.S. states, or regions of states, remain.

It is important to recognize and analyze the uncertainties about the history, extent, and limits of the native ranges of species such as the rusty crayfish, because determining native or non-native status for these species may have important implications for the ways in which the species are perceived and treated. Native species are often protected and viewed positively while non-native ones may become the subject of control and even attempted eradication programs (Guiaşu, 2016; Pereyra & Guiaşu, 2020). This may lead to the development of bias in ecological and conservation studies focused on non-native species, and an emphasis on the perceived negative impacts of these species, while ignoring or minimizing their potential positive contributions to ecosystems (Schlaepfer et al., 2011; Guiaşu, 2016; Guiaşu & Tindale, 2018). Thus, estimating the native or non-native status of species can be a highly subjective exercise, often based on incomplete and/or contradictory information. At the same time, assessments of the ecological impacts of species can also be quite subjective, and may be influenced by the perception of the native or non-native status of these species (Guiaşu, 2016).

The determination of the native or non-native status of the rusty crayfish may have an important role for the interpretation of the data in other types of studies—for example, behavioral and physiological studies as well. For instance, Hazlett et al. (2002) compared the memory capabilities of invasive and native crayfish species. Two of the paired species chosen for the study were *Faxonius rusticus*, as the invasive species in Michigan, and *Faxonius virilis*, as the native species in that same state. The study concluded that the supposedly invasive *F. rusticus* retained information longer than the native *F. virilis*, and on the basis of this conclusion, the authors offered the generalization that invasive species show greater behavioral plasticity than native species, which presumably gives the invasive species an advantage over the native ones. However, if *F. rusticus* turns out to be a native species in Michigan after all, as quite a few studies have stated (Table 1), then the general conclusion of the Hazlett et al. (2002) study would have to be reassessed.

**Conclusion**

*F. rusticus* has been intensely studied, particularly in the last few decades, undoubtedly at least in part because of its perceived invasive status. Given the ongoing debates and continuing controversies regarding the extent and history of the native range of the rusty crayfish, caution should be exercised and more conclusive evidence should be gathered, before making definitive pronouncements about the native or non-native status of this species at many locations. It is important to acknowledge that often we simply do not have enough information about the distributions of species, and, in many cases, the crucial relevant facts which would allow us to confidently decide whether a
species is native or not (assuming we think such a distinction matters) may never become available.

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Author contributions Radu Guias¸u initiated and designed the study and summarized and analyzed the data in Table 1 and some of the data in Table 2. Material preparation, data collection, and analysis were performed by Mark Labib and Radu Guias¸u. The final version of the manuscript was written mainly by Radu Guias¸u with contributions from Mark Labib. Both authors offered input on previous versions of the manuscript. Both authors read and approved the final manuscript.

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