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Harmful or useful? A case study of the exotic peregrine earthworm morphospecies *Pontoscolex corethrurus*

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A B S T R A C T

Exotic peregrine earthworms are often considered to cause environmental harm and to have a negative impact on native species, but, as ecosystem engineers, they enhance soil physical properties. *Pontoscolex corethrurus* is by far the most studied morphospecies and is also the most widespread in tropical areas. The term of morphospecies is used in this review because *P. corethrurus* may in fact constitute a complex of cryptic species. This earthworm is found in a wide range of habitats, from apparently pristine to any kind of human-disturbed environment. This review synthesizes 265 studies describing the distribution, morphology, biological and ecological traits of this morphospecies, as well as its impacts on soil conditions and communities. We then discuss the characteristics necessary for this specific morphospecies to become a successful colonizer throughout the world and the positive and negative effects it can have on the ecosystems that it has invaded. We emphasize the lack of knowledge of *P. corethrurus* reproductive mode and ploidy level, of its population genetics, and of the potential existence of cryptic species. To finish, we highlight the fact that data on *P. corethrurus* interactions with non-earthworm soil macrofauna are scarce.

1. Introduction

Earthworms are generally described as ecosystem engineers that greatly impact the physical, chemical and biological properties of soil (Blouin et al., 2013). Of the 3000–3500 earthworm species that have been described (Csuzdi, 2012), about 150 species are considered to be peregrine (i.e., widely ranging, often owing to human activity; Blakemore, 2012). Most of these peregrine earthworm species are well adapted to human transport and can colonize disturbed habitats (Hendrix et al., 2008). Climate may act as a barrier to their dispersal while their abundance may be limited by soil fertility and plant cover quality (Ortiz-gamino et al., 2016). It is also recognized that introduced species may cause changes to the ecosystem to which it has been introduced. For instance, European *Lumbricidae* such as *Lumbricus rubellus* or *L. terrestris* that have invaded previously glaciated regions in Canada and the USA have dramatically affected nutrient cycling and the functioning of the native ecosystems (Eisenhauer et al., 2011; Suárez et al., 2006).

Most of the species that are deliberately or inadvertently introduced into a new region fail to survive, and the majority of those that do survive, do not become invasive pests (Williamson and Fitter, 1996).

Introduced species pass through filters at four well-established spatio-temporal stages of invasion: introduction, establishment, landscape spread and integration (Vermeij, 1996). Species traits and environmental characteristics (Vermeij, 1996), as well as propagule pressure (propagule sizes, propagule numbers, and temporal and spatial patterns of propagule arrival) (Simberloff, 2009) may explain the success of these invasive species. Here, we discuss the case of *Pontoscolex corethrurus*, the quintessential peregrine earthworm in the tropics which has been successfully introduced worldwide. This endogeic earthworm tolerates a wide range of biotic and abiotic environmental conditions (Fragoso et al., 1999; Lavelle et al., 1987). It was first described in 1857 by Fritz Müller from Itajahy in the state of Santa Catarina in Brazil. Righi (1984) identified the Guyana shield as the original region of the *Pontoscolex* genus. Recently, Cunha et al. (2014), revealed the existence of two highly divergent genetic lineages within *P. corethrurus* in the island of Sao Miguel (Azores), suggesting the existence of cryptic species (i.e., different species which are not distinguishable morphologically). Thus, we choose to refer to the “morphospecies” *P. corethrurus* (i.e., a species distinguished from others only by its morphology) in this review. Cryptic species should be accounted for biological and ecological studies because different species may show differential

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adaptations to diverse environments and respond differently to perturbations.

P. corethrurus is one of the most studied tropical earthworm morphospecies in soil science (Fragoso et al., 1997; Plisko, 2001). It is used in ecotoxicological studies (Römbke and García, 2000), and it has been recommended as a bioindicator for the assessment of soil quality and ecosystem disturbances (Brown et al., 2006). Some restoration strategies of degraded soils have included the introduction of the morphospecies. For instance, it was used for the biofertilisation of tropical agricultural lands (Senapati et al., 1999; Topoliantz et al., 2002), the remediation of polluted sites (Duarte et al., 2012; Ganihar, 2003; García and Fragoso, 2002; Liang et al., 2011), and the improvement of phytoextraction treatments (Jusselme et al., 2012). Additionally, its use has been proposed in vermicomposting (Chaudhuri and Bhattacharjee, 2011; Molina-Murguía et al., 2009; Nath and Chaudhuri, 2012; Sabrina et al., 2013) and as a source of protein in animal feed for poultry and pork, and in fisheries (Brown et al., 2006). Although *P. corethrurus* may have a positive impact on soil ecosystems in certain circumstances, it may also negatively affect soil physical properties by increasing soil compaction. It may also modify biogeochemical processes as well as communities of plants, microbes and native earthworms (Marichal et al., 2010).

Four hypotheses have been put forward for explaining the success of invasive species: (i) they have traits that favour each stage of the invasion process, (ii) they exploit empty niches, (iii) they are favoured by anthropogenic pressure on natives and (iv) they are no longer under predatory, parasitic or competitive pressure (Sakai et al., 2001). Here, our objectives were (i) to address each of these hypotheses in order to describe the colonization success of the earthworm *P. corethrurus* in its pan-tropical region; due to the scarcity of data on the pathogens, parasites and predators of this species, the fourth hypothesis was not developed; (ii) to discuss the effects of the morphospecies in the introduced areas and (iii) to identify evidence in the literature suggesting the use of different cryptic species in experimental studies. We also identified knowledge gaps and provided promising perspectives for future research.

2. Literature search

The literature search was carried out using the keyword “*Pontoscolex corethrurus*” in Topics of the Web of Science databases using the ‘All Databases’ option. This option contained ‘Web of Science TM Core Collection’, ‘Current Contents Connect’, ‘KCI-Korean Journal Database’, ‘MEDLINE’, ‘SciELO Citation Index’ and ‘CABI’ research engines. We found 302 references published between 1900 and 2017. We also searched for synonymous species described by Blakemore (2006): *Lumbricus corethrurus*, *Urochaeta corethrura*, *Pontoscolex arenicola*, *Urochaeta hystrix*, *Urochaeta dubia*, *Urochaeta, sp.*, *Urochaeta australiensis*, *Pontoscolex hawaiiensis*, *Pontoscolex guangdongensis* and *Pontoscolex corethrurus mexicana*.

The articles written in English which were relevant for the review were sorted using the abstracts and the full texts. Moreover, the articles written in other languages and from which we could extract the information from the figures and tables, were also used. Finally, articles that did not focus specifically on *P. corethrurus* (e.g., when *P. corethrurus* was used for comparing results) were excluded. To complete the bibliographic corpus, some essential articles, which were not in the Web of Science, were collected from soil science specialists. The final corpus was composed of 265 references (Fig. 1). Most of the papers studied specimens collected outside the Guyana shield which is the putative native area of *P. corethrurus*. The greatest number of studies were conducted in India and Brazil, with 46 references each, followed by Mexico, with 39 references (Fig. 2).

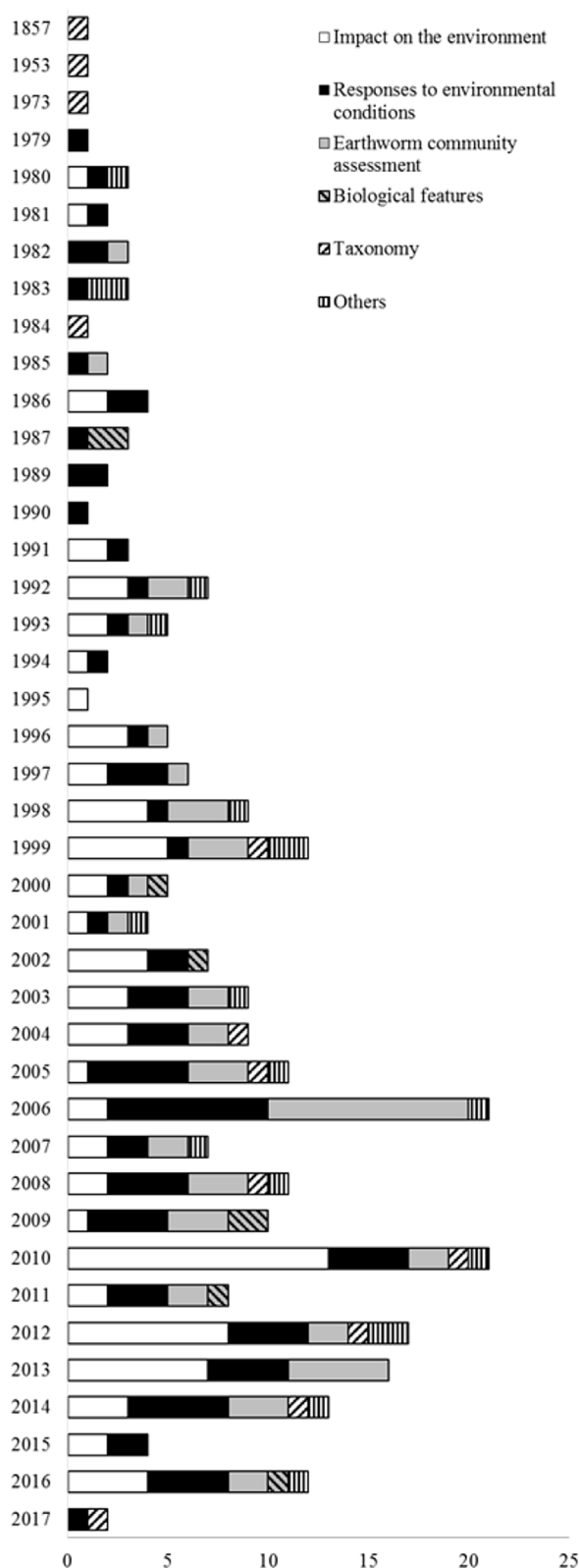


Fig. 1. Bibliographic corpus on *P. corethrurus* gathered in this review (source: ISI Web of Science). Papers were grouped into 6 different categories, corresponding to the most studied subjects on *P. corethrurus*: impact on the environment (33% of the studies), responses to environmental conditions (32%), earthworm community assessment (22%), biological features (3%), taxonomy (4%) and other subjects (i.e., genetics, biochemistry, geographical distribution and digestion) (6%).

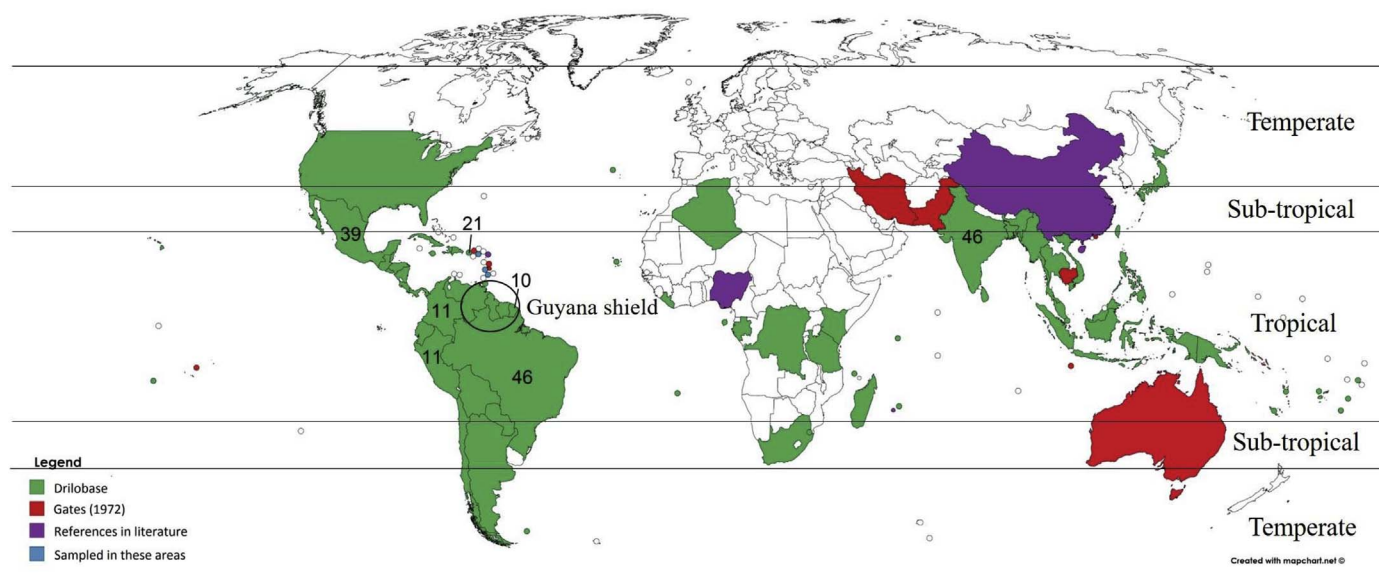


Fig. 2. Distribution map indicating the countries where *P. corethrusus* was found. Numbers show the countries where more than 10 studies were carried out on *P. corethrusus*. Four types of sources were used for this map and are presented in different colors: (i) in green, the locality specified in the Drilobase web site (<http://taxo.drilobase.org/>), (ii) in red, localities found in Gates (1972) but not mentioned in the Drilobase, (iii) in purple, four localities (China, Reunion and Guadeloupe islands, and Nigeria) found in the literature (China: (Hua et al., 2008; Huang et al., 2015; Paz-Ferreiro et al., 2015, 2014; Zhang et al., 2010), Reunion: (Boyer et al., 2013), Guadeloupe: (Lafont et al., 2007; Loranger-Merciris et al., 2012; Sierra et al., 2014), and Nigeria (Henrot and Brussaard, 1997; Mba, 1994); and (iv) in blue, three islands (St. Kitts, St. Lucia, St. Vincent) where *P. corethrusus* was sampled (S. James pers. com.) but this was not recorded in the literature. The map was done on <https://mapchart.net/> website. When *P. corethrusus* was recorded in a country, all the country is colored although the distribution of the species could be more restricted (for instance *P. corethrusus* is only present in the sub-tropical area of the United States). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3. General results

3.1. Distribution and dispersal vectors

Pontoscolex corethrusus has a widespread distribution, shown in Fig. 2. The map shows that it is present not only in tropical regions but also in sub-tropical zones. For instance, Ortiz-gamino et al. (2016) recorded its presence in sub-tropical regions of Mexico, at an elevation of 1550–1619 m above sea level (m.a.s.l.), and an average temperature of $17^{\circ} \pm 2$, where no other tropical species occur. This morphospecies was even recorded in the temperate zone, in the Azores archipelago (Cunha et al., 2014) and the Falkland islands (Reynolds and Jones, 2006). Gates (1972) mentioned that *P. corethrusus* was present in a greenhouse in the London suburb of Kew (United Kingdom), but there is no record of its expansion in this country.

Several vectors of passive dispersal may be involved in the spread of peregrine earthworms, e.g., transport of cocoons by streams and surface water, phoretic interactions with birds and mammals, transport by humans which can be accidental (with soil or potted plants) or commercial, for fishing bait and waste management industries (*P. corethrusus* is most probably extensively transported by humans). Dupont et al. (2012) proposed that the accidental transfer of this morphospecies from Cayenne to the Nouragues reserve in French Guiana, which was revealed using the Amplified Fragment Length Polymorphism (AFLP) method, could be due to deliberate soil transfer for scientific experiments and accidental soil transfer on tools and shoes. Moreover, Brown et al. (2006) indicated that *P. corethrusus* is commonly used as fish-bait in Brazil. While González et al. (2006) highlighted the fact that its dispersal to the Caribbean Islands can be explained by human migration prior to European colonization, Blakemore (2006) suggested oceanic drifting as another vector of dispersal.

3.2. Morphology

Our purpose was not to describe in detail *P. corethrusus* morphological diagnosis but instead to highlight the main external and internal

morphological traits mentioned in the literature. When reviewing 13 studies on *P. corethrusus* taxonomy (see Table 1 for references), we noticed some heterogeneity in the descriptions. For instance, some differences in the positions of the clitellum and tubercula pubertatis, which are key traits in earthworm taxonomy, were observed among papers. The beginning of the clitellum position has been identified in either XIV or XV segments while the end of it has been found in three different segments: XXI, XXII, and XXIII. The beginning of the tubercula pubertatis has been found in XV, XVIII and XIX segments and its ends in XXI, XXII and XXIII segments. Moreover, female, male and spermathecal pores have not always been observed (Table 1). Some traits were homogenous among references, such as the position of spermathecae and calciferous glands. The quincunx formation of setae on the last quarter of the body was mentioned in several studies. It is a character commonly used for the diagnosis of this species. However, Moreno (2004) highlighted the possibility of mistaking this species with others of the *Pontoscolex* genus by considering only this characteristic. Another diagnostic characteristic of the morphospecies is a special caudal zone described by Eisen (1896) and Gates (1973) of 4–7 segments (Table 1). The typhlosole which begins approximately at segment XXI ends with this caudal zone (Gates, 1973).

3.3. Morphospecies traits and environmental characteristics

3.3.1. Reproductive strategy and fecundity

Earthworms are usually hermaphrodites, meaning that both male and female organ systems, such as testes and ovaries, occur within a single individual. In *P. corethrusus*, male reproductive organs are often absent or atrophied (Gates, 1973; Tsai et al., 2000) and cocoons are viable without mating, thus suggesting a parthenogenetic reproduction (Chaudhuri and Bhattacharjee, 2011). In rare cases, Gates (1973) observed some iridescence in *P. corethrusus* spermathecae that raised the possibility of biparental reproduction. Sexual reproduction has also been suggested to occur by Dupont et al. (2012), based on a population genetics study.

This morphospecies is a continuous breeder with a high fecundity

Table 1

Morphological characteristics of *P. corethrurus* described in 13 papers focusing on its taxonomy. External and internal morphological traits mentioned in more than 3 references were recorded. The positions are based on segments.

Morphological traits	Descriptions	
External characteristics		
Body length (mm)	Minimum	60 (2,4,8), 92 (11, 13), 95 (3),
	Maximum	75 (8), 120 (4,2), 100 (10), 111 (3), 128 (13), 148 (11), 155 (12)
Segment numbers	Minimum	129 (12), 145 (3), 160 (10), 166 (2), 167 (5, 11, 13), 193 (8), 200 (6), 212 (4)
	Maximum	165 (12), 200 (2, 10), 210 (8), 212 (3), 220 (13), 222 (5), 232 (11), 250 (6)
Pigmentation	Absence	(2, 4, 6, 10, 11)
	Presence	Pale brown (12), white to pink (13)
Clitellum	Position	XV-XXIII (2, 3, 4, 5, 10, 12) XIV-XXII (11, 13), XV-XXI (8), XV-XXII (1)
	Shape	Saddle shaped (2, 4, 5, 7, 8, 11, 12, 13)
Tubercula pubertatis	Position	½ XIX- ½ XXIII (3), XIX-XXI (2, 8), XIX/n-XXI, XXII/n (4), XIX/2, XIX/n, XX to XXI, XXII/n (5), XIX- ½ XXII (10), XVIII-XXI (11), XIX-XXII (12), XV-XXI (13)
	Shape	Longitudinal bands of irregular shape (4, 11, 12)
Dorsal pore	Absent	(2, 11, 12, 13)
Female pore	Absence	(8, 11, 13)
	Presence	(2, 5, 6, 10, 12)
	Number	One pair (10)
	Position	XIV-XV (10)
Male pore	Absence	(5, 8, 11, 12)
	Presence	(2, 4, 7, 13)
	Number	One pair (10)
	Position	XIX/XX (2), intersegmental in XX-XXI (10), XVII (13)
Spermathecal pores	Absence	(11, 13)
	Presence	(2, 3, 5, 7, 10, 12)
	Number	Three pairs (7, 10, 12)
	Position	On intersegmental furrows of VI/VII-VII/VIII-VIII/IX (7, 10, 12), VI/VII-VIII/IX (2, 5)
Tail's quincunx formation of setae	Presence	(2, 4, 5, 7, 8, 10, 11, 12, 13)
Caudal zone	Position	CVII-CXVIII (3), CXIII-CXXXIII (5), CXX-CXXX (9),
	Number	4-7 (5), 5-7 (9) segments long
Internal characteristics		
Typhlosole	Presence	(2, 4, 5, 7, 10, 11, 12, 13)
	Caeca absence	(7, 11, 12, 13)
	Caeca presence	(2)
	Typhlosole position (start)	XXI-XXV (4), XXIII-XXV (10), XV (11, 13), XXII (12)
	Typhlosole position (end)	CVIII-CXXXVIII (5), CXIII-CXXV (10)
	Spermathecae	Number
	Position	VII-IX (2, 3, 5, 7, 8, 10, 11, 12, 13), VIII-IX (1)
	Shape	Club-shaped (8), tubular (11)

Table 1 (continued)

Morphological traits	Descriptions	
Seminal vesicles	Absence	(5)
	Presence	(2, 4, 5, 7, 10, 11, 12, 13)
	Number	One pair (2, 4, 10, 11, 12, 13), 8 to 10 segments long (4, 5)
	Position Shape	XII (2, 12), XV-XVII (11), XIII (13) Saccular (2, 12), follicular and flattened (11), taped shape (10)
Calciferous glands	Number	Three pairs (1, 2, 3, 5, 7, 8, 10, 11, 13)
	Position	VII-IX (1, 2, 3, 5, 7, 8, 10, 11, 12, 13)
	Shape	Lingular and flattened (2), oval shaped (11, 13), tubular (10, 12),

(1) (Beddard, 1893), (2) (Blakemore, 2006), (3) (Eisen, 1896), (4) (Gates, 1972), (5) (Gates, 1973), (6) (Müller, 1857), (7) (Narayanan et al., 2016), (8) (Nxele, 2012), (9) (Righi and Bittencourt, 1972), (10) (Righi, 1990) (11) (Shen and Yeo, 2005), (12) (Tripathi and Bhardwaj, 2005), (13) (Tsai et al., 2000).

rate (Gates, 1972; Vannucci, 1953). Under laboratory conditions, an adult of *P. corethrurus* can produce up to 145 cocoons per year (Arunachalam, 1987; Bhattacharjee and Chaudhuri, 2002; García and Fragoso, 2002). Cocoons have a short development time ranging from 21 ± 1 to 40 ± 9 days at 20–32 °C in laboratory (Arunachalam, 1987; Bhattacharjee and Chaudhuri, 2002; Chaudhuri and Bhattacharjee, 2011; Gates, 1972; Nair et al., 2009; Ortiz-ceballos et al., 2009). The hatching rate of cocoons is high, ranging from 78% to 97%, depending on the temperature, in moist soil conditions (Lavelle et al., 1987). Generally, one hatchling is present per cocoon (Bhattacharjee and Chaudhuri, 2002; Vannucci, 1953; but see Nair et al., 2009). Before depositing their cocoons, *P. corethrurus* individuals build spherical nest chambers (mean diameter of 5.97 ± 1.24 mm) with their buccal appendix and coat the chambers with a fine layer of soil and mucus (Ortiz-ceballos et al., 2009). Cocoons are then laid individually in these chambers (Hamoui, 1991; Vannucci, 1953). The nest chamber are surrounded by a 'feeding-chamber' where casts are deposited and where juvenile earthworms can come to feed once hatched (Ortiz-ceballos et al., 2009).

Research has revealed that *P. corethrurus* present a relative reproductive plasticity. For instance, this morphospecies has been shown to increase its rate of cocoon production and incubation period with increased temperature (Bhattacharjee and Chaudhuri, 2002). Moreover, García and Fragoso (2003) showed that individuals from the same population of *P. corethrurus* raised on different substrates displayed a possible physiological trade-off between cocoon number and cocoon weight, related to nitrogen (N) limitations. In their experiment, *P. corethrurus* produced fewer but bigger cocoons (> 50 mg) in soils with high N-availability and more but smaller cocoons (< 50 mg) when N was less available (García and Fragoso, 2003).

3.3.2. Feeding habits, soil nutrient content and plant composition of the ecosystem

The *P. corethrurus* diet is geophagous (i.e., feeding on soil) and can be classified between the polyhumic (i.e., ingesting soil with high organic matter content) and mesohumic (i.e., feeding indiscriminately on both mineral and organic particles) endogeic categories (Barois et al., 1999; Lavelle et al., 1987). Research has suggested that *P. corethrurus* may derive much of its tissue carbon (C) from rhizospheric sources (Spain et al., 1990) and fungal biomass may be its main source of N (Lachnicht et al., 2002).

Its abundance is positively affected by organic matter availability (García and Fragoso, 2002; Marichal et al., 2010; Ortiz-Gamino et al., 2016), N availability (Li et al., 2010; Marichal et al., 2010) and P availability (Marichal et al., 2011) in the soil. Therefore, this morphospecies prefers rich soils in terms of organic matter and leaf litter (Liu and Zou, 2002; Ganihar, 2003; García and Fragoso, 2003). It is,

however, worth noting that *Ayala and Barois (2016)* showed in a laboratory experiments that *P. corethrus* was unable to grow in an extremely rich substrate of 75–100% organic matter, the mortality rate being between 56 and 100%.

P. corethrus is also able to feed in environments where litter resources are low (*Lavelle et al., 1987; Marichal et al., 2010; Ponge et al., 2006; Shilenkova and Tiunov, 2015*). For instance, *P. corethrus* reached a remarkably high density (200 ind.m⁻²) in a soil extremely poor in organic matter, the alluvial sandy soil of a gallery forest along the Dong Nai River in the Cat Tien National Park, southern Vietnam. The results of a microcosm experiment suggested that the high abundance of these earthworms in poor sandy soils might be due to assimilation of labile carbon released to the soil from plant roots (*Shilenkova and Tiunov, 2015*).

Plant species differ in the quantity and quality of litter produced, and these differences may significantly affect earthworm populations (*Zou, 1993*): the density of *P. corethrus* was higher in Hawaiian plantations considered to have high litter quality (*Albizia falcataria* plantations) compared with plantations with lower litter quality (*Eucalyptus saligna*). Plants may affect earthworm populations in other ways; for instance *León and Zou (2004)* showed that the shift from grass vegetation (*Axonopus compressus*) to woody plants (*Miconia prasina*) in secondary forests of Puerto Rico decreased the abundance and biomass of *P. corethrus* through reducing fine root biomass.

3.3.3. Habitat

3.3.3.1. Vegetative cover. *P. corethrus* seems to proliferate in disturbed habitats (*Marichal et al., 2010*) and is often found to be dominant in croplands, pastures, urban areas and gardens (*Table 2*). However, *P. corethrus* has also been found in forests (*Table 2*). In particular, it was found to be dominant in the primary forests of the Manzillo Wildlife Refuge and of the Tortuguero National Park in Costa-Rica (*Lapied and Lavelle, 2003*), in the tropical rainforests of Puerto-Rico (*Zou and González, 1997*) and in the cloud forest at the top of Luquillo Mountains (*Liu and Zou, 2002*), a result highlighting that this species also lives in undisturbed ecosystems.

3.3.3.2. Soil moisture and temperature. *P. corethrus* populations are generally found in areas where the annual mean temperature is above 20 °C. Reproduction being restricted to the 23–27 °C range, *P. corethrus* growth to the adult stage is only possible between 20° and 30 °C (*Lavelle et al., 1987*). Contrary to other tropical species (e.g., *Meroscolex marculi* and *Andiorrhinus caudatus*), *P. corethrus* is resistant to dehydration (*Ayres and Guerra, 1981*). However, if the soil moisture is too low (depending on the soil type), *P. corethrus* may go into diapause (i.e., temporary suspension in development) (*Chuang et al., 2004; Guerra, 1994*). The use of soil moisture treatments as a gradient of “optimal-stress” environmental conditions by *Fragoso and Lozano (1992)*, showed that juveniles and adults of *P. corethrus* use different strategies for tissue regeneration. In juvenile worms, caudal amputation resulted in the initiation of diapause and, consequently, in the activation of the process of regeneration, independently of environmental conditions. Adults were only capable of regenerating tissue during diapause, which mainly occurred under conditions of environmental stress (soil dryness in the experiment). In a laboratory experiment, *Zhang et al. (2008)* showed that soil dryness was the primary factor limiting the reproduction of *P. corethrus*.

3.3.3.3. Soil physico-chemical characteristics. Although *P. corethrus* is found in a wide range of soil types (e.g., Entisol-Oxisol, Vertisol, Ferrasol, Ultisol, Fluvisol, and Andosol soils), *Huerta et al. (2007)* showed in Tabasco, Mexico that it prefers sites with high silt content (Fluvisol). It tolerates a wide range of soil pH (*García and Fragoso, 2002; Lavelle et al., 1987*) and, although it is often found in relatively acidic soil i.e., from 4.5 to 6.8 (*Table 2, Teng et al., 2013*), it favors soils with higher pH. Studying a wide range of deforested soils of Eastern

Amazonia, *Marichal et al. (2010)* revealed that *P. corethrus* densities covaried with pH and also with silt. Although it seems to favour soils with high pH, *Marichal et al. (2012)* found a positive relationship between mortality and pH in soil sampled in Eastern Brazilian Amazonian soils with high pH values (7.41 and 7.96). Juveniles seem more sensitive to pH than adults; *Topoliantz et al. (2005)* found that treatments increasing pH, such as charcoal addition, promoted juvenile activity (i.e., casting).

3.3.3.4. Soil contaminants. *Zavala-Cruz et al. (2012)* proposed that the ability of *P. corethrus* to colonize contaminated soils could be favoured by a genetic plasticity that confers a certain tolerance to pollutants or a specific genetic resistance to pollutants. *P. corethrus* has indeed a broad tolerance towards soil contaminants and has been found in different polluted sites. For instance, *P. corethrus* was the most abundant morphospecies (75% of the total abundance of the community) in a site contaminated with hydrocarbons after an oil spill about 20 years previously in Tabasco, Mexico (*Hernández-Castellanos et al., 2013*), suggesting a high tolerance to benzo(a)pyrene (BaP).

A similar tolerance to trace elements has been reported by *Duarte et al. (2014)* in a lead (Pb) mining site in Southern Brazil. They showed that *P. corethrus* biomass, cast production and survival rates were reduced only at high Pb soil concentrations (9.716 µg g⁻¹), compared to low and intermediate Pb concentrations (maximum 4.278 µg g⁻¹). Similarly, *P. corethrus* mortality, growth and cocoon production were affected only at high mercury (Hg) concentrations (50 and 100 µg g⁻¹ soil) after 56 days in a laboratory experiment with soils from forested sites in French Guiana (*Da Silva et al., 2016*). *Buch et al. (2017)* worked on soils of two Brazilian forest conservation units that had been polluted by Hg due to atmospheric deposition. They found cocoon production and earthworm growth to be affected at much lower concentrations of Hg i.e., 8 µg g⁻¹ than that reported by *Da Silva et al. (2016)*. At this concentration, *P. corethrus* individuals were not found to avoid the contaminated soil. As with other contaminants and earthworm species (*Pelosi et al., 2014*), the bioavailability of chemicals in soils is highly dependent on soil properties (*Van Gestel and Weeks, 2004*). Therefore, the effects of trace elements on *P. corethrus* are likely to depend on soil type, moisture, temperature and many other soil characteristics.

Only a few studies have investigated *P. corethrus* sensitivity to pesticides. *Kale and Krishnamoorthy (1979)* assessed the effects of the insecticide Sevin (i.e., 1-naphthyl-*n*-methylcarbamate) which was mixed with a clay loam in the laboratory. They found the lower concentrations (i.e., 37.5–75 ppm) to have a stimulatory effect on earthworm growth and survival rather than an inhibitory effect. However, the highest concentrations (i.e., > 150 ppm) resulted in growth delays and reduced rates of survival. *Forster et al. (2006)* showed that *P. corethrus* was very sensitive to the fungicide carbendazim. This fungicide, forbidden in Europe since 2009, caused a decrease in *P. corethrus* abundance during a three-month experiment under laboratory conditions using intact soil-core terrestrial model ecosystems (TMEs). This result was confirmed by *Buch et al. (2013)* who revealed that carbendazim at 3.16 mg a.i.kg⁻¹ and the insecticide carbofuran at 5 mg a.i.kg⁻¹ applied in boxes filled with artificial tropical soil (TAS, a substrate used in ecotoxicological tests (*OECD, 1984*)) had lethal effects on this morphospecies.

Finally, the response of *P. corethrus* to herbicides is variable, as it is for the other contaminants mentioned above. Even at the highest concentrations of a glyphosate-based herbicide (GBH) (47 mg a.i.kg⁻¹), *Buch et al. (2013)* did not find any significant effect on mortality. Conversely, *García-Pérez et al. (2014)* showed that GBH could have lethal impacts on *P. corethrus*, as the application of GBH to coffee plantations thrice a year caused significant reduction in *P. corethrus* density (167 and 353 ind.m⁻² with and without herbicide, respectively) and biomass (23 and 45 g m⁻² with and without herbicide, respectively). However, in another study under laboratory conditions

Table 2

Relative abundance and dominance status of *P. corethrurus* based on papers published since 2000. The relative abundance of other species (sp.) is also presented. When the information was available, it is indicated when the species was considered dominant (D).

Habitat	Country	Soil pH	Relative abundance (%)				Ref ^a	
			<i>P. corethrurus</i>	other exotic sp	native sp	undefined origin sp		
Forest	Secondary forest	Brazil	-	25.0	75.0	-	-	1
	Disturbed native forest	Brazil	5	-	100	-	-	2
	Forest of the Cahuita National Park	Costa Rica	-	68.2 (D)	31.8	-	-	3
	Peripheric primary forest of Tortuguero National Park	Costa Rica	-	100 (D)	-	-	-	3
	Primary forest of the Manzanillo Wildlife Refuge	Costa Rica	-	91.4 (D)	8.6	-	-	3
	Remote primary forest of Tortuguero National Park	Costa Rica	-	-	-	100	-	3
	Forest	Cuba	5.62	65.8 (D)	21.4	12.8	-	4
	Mixed forest	India	4.62	28 (D)	22.3	49.7	-	5
	Elfin woodland	Puerto Rico	-	14.7	16.5	68.8	-	6
	Flooded <i>Pterocarpus</i>	Puerto Rico	-	-	-	100	-	6
	Lowland moist forest	Puerto Rico	-	51.5	34	14.5	-	6
	Lowland dry forest	Puerto Rico	-	-	100	-	-	6
	Palo colorado forest	Puerto Rico	-	51.7	-	48.3	-	6
	Sierra palm forest	Puerto Rico	-	85.7	2.4	11.9	-	6
	Tabonuco forest	Puerto Rico	-	80.2	2.4	17.4	-	6
	Forest with coffee (<i>Coffea arabica</i>)	Puerto Rico	6.7–6.8	100 (D)	-	-	-	7
	Forest with fern (<i>Dicranoteris flexusosa</i>)	Puerto Rico	5.8–6.8	100 (D)	-	-	-	7
	Forest with <i>Selaginella</i> spp.	Puerto Rico	5.3–5.9	79.0 (D)	-	21.0	-	7
	Maricao State Forest	Puerto Rico	4.5–5.0	98.0 (D)	-	2.0	-	8
	Wet forest (well-drained areas)	Puerto Rico	4.7	97.0 (D)	-	1.0	2.0	9
	Wet forest (Tabonuco forest)	Puerto Rico	5.9	95.0 (D)	-	-	5.0	9
	Fresh water swamp forest	Singapore	-	86.0	-	-	14.0	10
	Bukit Timah nature reserve (foret)	Singapore	-	12.5	-	-	87.5	10
Upper seletar resevoir park (foret)	Singapore	-	91.6	-	-	8.4	10	
Dry evergreen forest	Thailand	-	58.8	-	-	41.2	11	
Dry dipterocarp forest fired	Thailand	-	-	-	-	100	11	
Dry dipterocarp forest-non fired	Thailand	-	-	-	-	100	11	
Wetland	Sungei buloh wetland reserve (covered with mangroves)	Singapore	-	87.2	-	-	12.8	10
Pasture and grassland	Cultivated pasture	Brazil	5.3	50.0	50.0	-	-	2
	Perennial pasture	Brazil	4.6	-	100	-	-	2
	Old pastures 1	Brazil	-	43.0	39.0	18.0	-	1
	Old pastures 2	Brazil	-	96.0 (D)	2.1	1.9	-	1
	Pasture	Cuba	5.6	11.3	74.8 (D)	13.9	-	4
	Pasture (extensive cattle farming) 1	Mexico	6.6	19.6	-	80.4	-	12
	Pasture (extensive cattle farming) 2	Mexico	6.6	37.0	63.0	-	-	12
	Pasture (semi-intensive cattle farming) 1	Mexico	5.5	46.0	54.0	-	-	12
	Pasture (semi-intensive cattle farming) 2	Mexico	5.6	-	100	-	-	12
	Rifle range (grass field)	Singapore	-	54.1	-	-	45.9	10
	Grassland	Thailand	-	55.6	-	-	44.4	11
Culture and plantation	Grain crop (converted from an old pasture)	Brazil	-	87.0 (D)	8.3	4.7	-	1
	Grain crop field 1	Brazil	-	0	66.5	33.5	-	1
	Grain crop field 2	Brazil	-	0	30.0	70.0 (D)	-	1
	Sugarcane (<i>Saccharum</i> sp.) 2	Brazil	-	10.0	60.0	30.0	-	1
	Sugarcane (<i>Saccharum</i> sp.) 1	Brazil	-	41.0	50.0	9.0	-	1
	Manduirana plantation	Brazil	5.6	-	100	-	-	2
	Banana plantation	Costa Rica	-	100 (D)	-	-	-	3
	Mixed fruit plantation	India	-	20.0	8.3	71.7 (D)	-	13
	Pineapple plantation	India	-	10.4	1.9	87.7 (D)	-	13
	Rubber plantation	India	4.7	71.8 (D)	5.4	22.8	-	14
	Rubber plantation	India	4.5	76.5(D)	3.3	20.2	-	5
	Agricultural ecosystem	Malaysia	6.1	7.8	-	-	92.2 (D)	15
	Rice paddy	Thailand	-	27.3	-	-	72.7	11
	Cassava plantation	Thailand	-	55.8	-	-	44.2	11
	Forest plantation	Thailand	-	93.3	-	-	6.7	11
	Mango plantation	Thailand	-	71.4	-	-	28.6	11
Sugarcane plantation	Thailand	-	-	-	-	100	11	
Urban area and gardens	Lawn	Brazil	4.6	25.0	75.0	-	-	2
	Bribri village	Costa Rica	-	100 (D)	-	-	-	3
	Cahuita village	Costa Rica	-	91.8 (D)	8.2	-	-	3
	Puerto Viejo village	Costa Rica	-	89.7 (D)	10.3	-	-	3
	Campus of National University of Singapore	Singapore	-	16.7	-	-	83.3	10
	Kranji wireless station	Singapore	-	80.8	-	-	19.2	10
	Singapore botanic gardens	Singapore	-	91.7	-	-	8.3	10
	Household area	Thailand	-	27.2	-	-	72.8	11
	Office building area 1	Thailand	-	52.0	-	-	48.0	11
	Office building area 2	Thailand	-	51.0	-	-	49.0	11

^a References: (1) (Nunes et al., 2006), (2) (Ressetti, 2006), (3) (Lapied and Lavelle, 2003), (4) (Martinez and Sanchez, 2000), (5) (Chaudhuri and Nath, 2011), (6) (González et al., 2007), (7) (Borges et al., 2006), (8) (Hubers et al., 2003), (9) (González et al., 1999), (10) (Shen and Yeo, 2005), (11) (Somniyam and Suwanwaree, 2009), (12) (Ortiz-gamino et al., 2007).

by the same authors, earthworms exposed to a *Coffea* litter polluted by GBH produced the same number of cocoons as *P. corethrus* fed with the unpolluted litter (García-pérez et al., 2016).

3.4. Impact of *P. corethrus* on its environment

3.4.1. Physical impacts on soil structure

P. corethrus is known to compact soil. As a consequence of its feeding activity, small aggregates are progressively transformed into larger aggregates which tend to accumulate in the absence of other agents that break down these larger aggregates; the soil is thus progressively compacted (Alegre et al., 1996; Blanchart et al., 1997). The accumulation of casts by *P. corethrus* at the soil surface under moist soil conditions may result in the formation of a continuous muddy layer of earthworm casts if “decompacting” activities by other invertebrate populations are too weak. The growth of plants is then prevented and when droughts occur, this layer turns into a compact thick crust. As a consequence, large patches of bare soil impermeable to water and air are generated (Chauvel et al., 1999). Alegre et al. (1996) observed a significant increase in bulk density from 1.12 to 1.23 g cm⁻³ and a decrease in porosity from 58% to 53% in the presence of *P. corethrus* in a loamy soil in Peru. Similar changes were found in a reciprocal transplant study by Barros et al. (2001) where blocks of forest soil with 48% porosity (in an experimental station in Central Amazonia in Brazil) were transferred to a pasture with 16% porosity where *P. corethrus* was very abundant (400 ind.m⁻²) and vice versa. After 1 year, the transplanted blocks of forest soil presented a porosity of 26%, whilst the transplanted blocks of pasture soil presented a porosity of 34%.

By contrast, in certain circumstances, *P. corethrus* contributed to soil bioturbation processes and decreased soil compaction. Zund et al. (1997) demonstrated that the presence of *P. corethrus* decreased bulk density and increased aeration of a compacted Oxisol from Australia. Moreover, Hallaire et al. (2000) showed, in a sandy loam soil in Yurimaguas, Peru, that *P. corethrus* activity induced a compaction of the surface soil, through a coalescence of casts, in plots without organic inputs whereas they created a crumb structure in plots with high soil organic matter contents. Although it is generally accepted that soil compaction by macroaggregation occurs when soil organic matter (SOM) is missing, Sparovek et al. (1999) showed that *P. corethrus* inoculation, with or without organic matter amendment, resulted in soil compaction in an acidic Oxisol of Brazil.

3.4.2. Chemical impacts

3.4.2.1. *Organic matter mineralization and nutrient cycling.* Earthworm activity via the production of casts is recognized as an important factor affecting C, N and phosphorus (P) cycles in the soil and CO₂ and N₂O fluxes from the soil to the atmosphere (Chapuis-Lardy et al., 2010; Jiménez et al., 2003; Lavelle et al., 1998). The activity of such endogeic geophagous earthworms is often considered to increase C mineralization in the short term and favour C storage through the stabilization of SOM in stable micro-aggregates in the long term (Lavelle et al., 1997; Lavelle and Martin, 1992; Lavelle and Spain, 2001). The influence of earthworms on SOM and nutrient dynamics may depend on a number of factors including the time frame in question but also inherent soil properties, the form of management in place (Fonte et al., 2010) and the interaction with plants (Fonte et al., 2012). Using microcosm experiments, Fonte et al. (2010) showed that, in the first 15 cm layer of the soil, *P. corethrus* decreased the total soil C by 3% under the Quesungual slash-and-mulch agroforestry system of western Honduras (QSMAS). The QSMAS is an agricultural system with short fallow periods and promoted by extension agents with the intention of reducing the slash-and-burn agricultural strategy (Pauli et al., 2005). By comparing treatments with and without earthworms in maize crops under no tillage in the Peruvian Amazonia, Desjardins et al.

(2003) showed that the total carbon content of the 0–10 cm depth was dramatically reduced by 28% in the earthworm – inoculated plots. The results of a 5 months incubation of *P. corethrus* with added rice and soybean residues suggested that incorporation of organic C by earthworm was higher with smaller rice residues than with larger and woodier soybean residues (Coq et al., 2007).

Earthworm activity is recognized to be an important factor in regulating CO₂ fluxes from the soil to the atmosphere (Speratti and Whalen, 2008). We found only one laboratory study investigating this issue with *P. corethrus*. The study showed that its presence in Ferralsol of Madagascar induced a significant increase in CO₂ emissions (Chapuis-Lardy et al., 2010).

In addition to its effects on C dynamics, *P. corethrus* is known to enhance N mineralization and availability (Araujo et al., 2004; González and Zou, 1999; Lafont et al., 2007; Lavelle et al., 1992; Tapiacoral et al., 2006). For instance, Lavelle et al. (1992) showed that mineral N concentrations ranged from 133.1 to 167.8 µg N per gram dry soil in fresh casts of this morphospecies fed on an Amazonian Ultisol. This was approximately five times higher than the concentration in the non-ingested soil. Similarly, Pashanasi et al. (1992) and Araujo et al. (2004) found that the introduction of *P. corethrus* significantly increased the soil microbial biomass-N (bio-N) and mineral-N availability in various experiments. However, in a mesocosm experiment, Fonte and Six (2010) found no significant effect of *P. corethrus* on potentially mineralizable N using a method that measured relatively labile sources of organic N.

Finally, it is generally accepted that earthworms increase P availability across a wide range of agroecosystems (Jiménez et al., 2003; Lopez-Hernandez et al., 1993). A significant increase of exchangeable phosphate was observed in the casts of *P. corethrus* in several experiments carried out in mesocosms using topsoil dug to a maximum of 25 cm depth (Chapuis-Lardy and Brossard, 1995; Chapuis-Lardy et al., 1998, 2009; Lopez-Hernandez et al., 1993; Sabrina et al., 2013), thus confirming its important contribution to phosphate cycling in tropical soil surface layer. Surprisingly, Fonte and Six (2010) observed a decrease in P availability in presence of *P. corethrus* in the surface 15 cm of mesocosms that were incubated under field conditions within the QSMAS in western Honduras. They proposed that increased P enrichment and availability in casts comes at the expense of lower P content and availability in non-ingested soil.

3.4.2.2. *Metal mobility and availability in soils.* In general, earthworms increase the availability and mobility of essential (e.g., Zn, Cu, Mn, Fe) and non-essential (e.g., Cd, Pb, Hg) metals in both contaminated and uncontaminated soils (Sizmur and Hodson, 2009). Using a sequential extraction procedure, Duarte et al. (2012) revealed that *P. corethrus* significantly reduced the amount of Pb in the soluble and exchangeable forms in the soil, and increased the Pb bound in Fe and Mn oxides in the casts. This can be beneficial for soil bioremediation. In addition, Jusselme et al. (2015) found that *P. corethrus* has an indirect impact on the Pb phytoextraction ability of *Lantana camara*. The presence of earthworms enhanced *L. camara* biomass by about 1.5–2 times, thereby increasing the uptake of Pb two to threefold (Jusselme et al., 2015).

3.4.3. Impact on biotic factors

3.4.3.1. *Effect on other earthworm species.* *Pontosclex corethrus* may reach high densities in some areas. Marichal et al. (2010) surveyed 270 sites in Brazil and Colombia and showed that where *P. corethrus* occurred, its average density was 90.2 ind.m⁻², ranging from 5.3 to 567 ind.m⁻². The density of *P. corethrus* populations is often inversely correlated with the density of other earthworm species (Chaudhuri and Nath, 2011; González et al., 1996; Lapied and Lavelle, 2003; Römbke et al., 2009).

Some studies have suggested that an increase in density of *P.*

corethrus could cause the loss of native species populations (Fragoso et al., 1995; Lapiéd and Lavelle, 2003). However, the coexistence of this morphospecies with native species has been observed in several sites of different forests in Cuba, India, Puerto Rico, in pastures in Brazil, Cuba and Mexico and in cultures and plantations in Brazil and India (Table 2). The coexistence or replacement of native earthworms by exotic ones may depend on the disturbance history and the state of naturalness of the landscape (González et al., 2006). Different relationships among *P. corethrus* and native earthworms may depend on the specific context of the study area. For instance, in a mid-altitude Tabonuco forest (400 m above sea level) in Puerto Rico, Hendrix et al. (1999) showed that the niches of *P. corethrus* and the native earthworm *Estherella* sp. Overlapped completely in sites rich in N resources. On the other hand, in a tropical forest in Puerto Rico, Lachnicht et al. (2002) found the activity of *Estherella* sp. and *P. corethrus* to be spatially separated, and it appeared that they excluded each other from bottom and surface layers. Marichal et al. (2010) suggested that the replacement of native species by *P. corethrus* is a result of changes in the environment, such as deforestation in tropical rainforest areas, that affect both groups of species differently, rather than the result of competition between invasive and native species. They proposed that while native species tend to disappear because of the destruction of their habitats and reduction of their food sources, *P. corethrus* can occupy the soil with increased pH, C and nutrient contents created by the deforestation and burning.

In some cases, the dominance of native species over *P. corethrus* was found, such as in pineapple plantations of West Tripura in India where the endogeic native species *Drawida assamensis* was dominant although *P. corethrus* was present (Table 2, Dey and Chaudhuri, 2014).

Lastly, *P. corethrus* may coexist with other exotic earthworm species (Table 2) such as *Dichogaster* spp in Brazil and Costa Rica (Lapiéd and Lavelle, 2003; Nunes et al., 2006), *Ocnoderilus occidentalis* and *Drawida barwelli* in Puerto Rico and Cuba (González et al., 2007; Martínez and Sanchez, 2000) *Amyntas gracilis* and *Octolasion tyrtaeum* in Mexico (Ortiz-gamino et al., 2016) and *Metaphire houlleti*, *M. posthuma*, *Perionyx excavatus* and *Amyntas alexandri* in India (Dey and Chaudhuri, 2014).

3.4.3.2. Effect on nematodes. Earthworms can have either a direct (e.g., by ingestion) or an indirect (i.e., by physical and chemical changes of soil properties) impact on plant-feeding nematodes (Blouin et al., 2005; Lafont et al., 2007; Senapati, 1992; Wurst, 2010). Under laboratory conditions, Boyer et al. (2013) revealed a decrease in *Heterodera sacchari* and *Pratylenchus zae* populations, two plant parasitic nematodes, in the presence of *P. corethrus*. They highlighted a transit effect on nematode populations during the passage through the earthworm gut. However, Lafont et al. (2007) and Loranger-Merciris et al. (2012) found that the density of the banana feeding nematodes *Radopholus similis*, *Pratylenchus coffeae* and *Helicotylenchus multincinctus* did not significantly decrease in presence of *P. corethrus* in microcosm experiments, although they observed significantly less root damage induced by nematodes. Finally, *P. corethrus* may have a positive effect on total nematode densities, as shown by Villenave et al. (2010) in a 5-month field mesocosm experiment conducted in Madagascar. The authors revealed that *P. corethrus* stimulated the microbial community, which increased the density of the dominant microbiovorous bacterial-feeding and fungal-feeding nematodes.

3.4.3.3. Effect on soil microorganisms. Endogeic earthworms have developed complex interactions with soil microorganisms. In particular, the digestion process in the earthworm gut is known to enhance microbial activity (Barois and Lavelle, 1986; Drake and Horn, 2007). The feeding activity of *P. corethrus* has been shown to result in increased microbial biomass and activity in casts after soil was passed through the gut and excreted (Barois, 1992; Barois and Lavelle, 1986;

Bernard et al., 2012). Thus, *P. corethrus* has provided a basis for the ‘sleeping beauty’ hypothesis where water and soluble-C in the form of intestinal mucus produced by the earthworm awakens dormant microbial communities in the gut, thereby increasing mineralization of the stable forms of SOM ingested (Lavelle et al., 1983). While dormant microorganisms may be activated during their transit through the gut, others remain unaffected, and yet others digested in the intestinal tract (Drake and Horn, 2007). Barois (1992) pointed out dissimilarities of gut microbial activity among *P. corethrus* populations suggesting that different populations might show differences in physiological genetics and/or in the intensity of the mutualism with the soil microbial communities. This latter study also demonstrated that temperature has a direct effect in triggering microbial activity within the gut of *P. corethrus*.

3.4.3.4. Effect on plants. Earthworms generally have positive effects on plant growth in the tropics (Brown et al., 1999) by affecting soil macroaggregation and availability of nutrients. We previously highlighted (section 3.4.1) that soil macroaggregation by *P. corethrus* often resulted in increased soil bulk density, and decreased total soil porosity and water infiltration, along with some changes in the soil moisture patterns. Such changes in a sandy loamy soil might be beneficial to some crops such as shown by Alegre et al. (1996) for rice cowpea and maize. Pashanasi et al. (1996) showed that the inoculation of *P. corethrus* at a density of 90 ind.m⁻² had a positive effect on soil properties and plant production in low-input cropping systems at Yurimaguas (Peru), although this positive effect varied depending on rainfall, plants and organic inputs. In particular, maize seemed to respond better than rice to earthworm effects, while cowpea did not respond at all.

A major factor affecting plant growth, in relation to the presence of earthworms, is the availability of resources. If the casts, which are enriched in nutrients necessary for plant growth such as N, P, and potassium (K) (Chaudhuri et al., 2012; Lopez-Hernandez et al., 1993) are deposited close to plant roots, they can have significant positive impacts on plant growth (Lavelle et al., 1992). For instance, Loranger-Merciris et al. (2012) showed that *P. corethrus* enhanced dessert banana growth through increased P availability in its casts. In another study, the presence of *P. corethrus* increased aboveground biomass of *Brachiaria decumbens* by 30%, via increased availability of soil nutrients (Fonte et al., 2012).

The activity of *P. corethrus* may also promote plant health. Teng et al. (2016) demonstrated that the severity of banana blood disease (i.e., a destructive bacterial infection caused by *Ralstonia solanacearum*) decreased after the inoculation of *P. corethrus*. This process was explained by a higher plant biomass in comparison to controls, as roots were exposed to high densities of beneficial microorganisms through burrowing and casting activities of the earthworms (Teng et al., 2016).

4. Discussion

4.1. Components of *P. corethrus* invasion success

Identifying traits correlated with invasiveness is a central goal in invasion ecology. It is generally agreed that distinct characteristics are important during different stages of the invasion process (e.g., Ribeiro et al., 2008). In particular life history traits (i.e., traits involved in reproduction, growth and survival) may help to differentiate potentially successful and unsuccessful invaders (Sol et al., 2012). During the first stage of the invasion, which is the arrival of a species in a new habitat, one or more propagules of a species must first be carried and survive the dispersal. Most long-distance introductions of *P. corethrus* to new areas are the direct or indirect result of human activities. This earthworm was thus transported throughout the world (Fig. 2) and these events that were probably recurrent are extremely difficult to date.

Once propagules are introduced, a successful invader must establish

a reproducing population. *P. corethrus* is a continuous breeder with a high fecundity rate, a high hatching success and a short development time (Lavelle, 1981). Organisms with such characteristics are often classified as r-selected and recognized to be frequently colonizing species (Bufford and Daehler, 2011). The fact that *P. corethrus* can reproduce by parthenogenesis predisposes this species to invasiveness. Indeed, the ability of a single individual to establish a population is an important characteristic of many invasive species (e.g. Dybdahl and Drown, 2011). Yet, parthenogenetic species lack the capacity to generate novel genetic variation necessary for evolvability (i.e., the ability of a population to adapt in response to environmentally induced stress, Waddington, 1965) due to the absence of bi-parental reproduction and genetic recombination. It has been suggested however, that *P. corethrus* is capable of bi-parental reproduction (Dupont et al., 2012; Gates, 1973). Such a mixed-mating system, allowing reproduction through inbreeding and outbreeding according to mating possibilities, is a trait that may favour the rapid establishment of an exotic species in new areas (Dupont et al., 2007). The possibility of sexual reproduction should be investigated by genotyping parents and offspring from cross experiments. Moreover, knowledge of the ploidy level of *P. corethrus* could help to better understand its reproductive mode. Indeed, parthenogenesis is closely linked to polyploidy in earthworms and odd number of chromosomes are often incompatible with sexual reproduction (Shen et al., 2011).

Competitive ability is another trait that may confer an advantage for invasive species during establishment. Many studies have documented invaders that show a superior ability to exploit local resources when compared with native residents (Sakai et al., 2001). Plasticity, i.e., the ability of an organism to cope with a wide variety of habitats and conditions, is thus an important factor in the success of the establishment step (Bufford and Daehler, 2011). *P. corethrus* is described as euryecic (i.e., of wide ecological plasticity). For instance, *P. corethrus* has a broad tolerance towards soil contaminants. Its fitness (i.e., individual reproductive success to participate in next generation pool gene) in different polluted sites is affected only at high pollutant concentrations. *P. corethrus* also presents a reproductive plasticity; an adjustment of cocoon production (number and weight) and incubation period have been observed in different situations (Bhattacharjee and Chaudhuri, 2002; García and Fragoso, 2003).

Another important sign of plasticity of this species is its flexible diet. Although *P. corethrus* prefers rich soils in terms of organic matter and leaf litters, it is able to proliferate in extremely poor soils (Shilenkova and Tiunov, 2015). Marichal et al. (2010) proposed that *P. corethrus* can occupy soils where other earthworm species are not present or have disappeared due to soil use and management.

In addition to the invasiveness of the species, another component of the invasion success is the invasibility of the recipient ecosystem (Mitchell et al., 2006). The hypothesis of ecological opportunity proposes that extinction of native species, and in consequence the creation of 'empty' niches, promote the establishment of exotic species (Elton, 1958). Since human-caused environmental changes may alter native species survival, they may favour a few introduced species that would competitively displace many other species from a region (Tilman and Lehman, 2001). Land use history plays thus a major role in determining the abundance and community structure of earthworms and the establishment of exotic earthworms in areas previously inhabited by native worms. For example, in the tropics, the conversion of forest to pastures has been associated with significant decreases in soil macro-invertebrate diversity (Lavelle and Pashanasi, 1989) and an increased dominance of a few exotic earthworm species that can persist along gradients of plant succession after disturbance (León et al., 2003; Zou and González, 1997). Although invasion by *P. corethrus* has been also observed in undisturbed habitats (González et al., 2006; Hendrix et al., 1999), it seems that land use conversion is a main reason for *P. corethrus* dominance in different parts of the world (Marichal et al., 2010; Zou et al., 2006).

Once initial colonization and establishment have occurred, invasive species may spread from long- and short-distance dispersal. The rate of range expansion will obviously be influenced by propagule pressure and dispersal capacity but also by the ability of individuals to survive and reproduce in the new range where the invasive species may encounter novel selective regimes (Sakai et al., 2001). The evolution of such local adaptation requires genetic variation. Little is known about the genetic composition of *P. corethrus* populations. Studies of population genetics might provide valuable information about the process of invasion, for instance by comparing the genetic composition of recently established populations with populations in the native range.

The last phase of the invasion process is the integration of the species in the ecosystem and its impact on the environment. The impact of *P. corethrus* on soil physical structure may be either detrimental or beneficial. Depending on the SOM content, its activity may either promote soil compaction, especially when populations of other "de-compacting" species are not present, or contribute to soil bioturbation (Hallaire et al., 2000). Moreover, *P. corethrus* is known to accelerate biogeochemical fluxes (González et al., 2006). In particular, its casting activity may increase the N and P availability in agroecosystems. *P. corethrus* presence may thus be beneficial for plant growth. Teng et al. (2016) also demonstrated its positive effect on plant health.

The impact of *P. corethrus* on other earthworm species and in particular on native species is still an open question. Some studies have stated that an increase in densities of *P. corethrus* might directly cause the disappearance of native species and that once established in areas inhabited by native species, its effects on soil properties prevent the recolonization by native species populations (Fragoso et al., 1995; Lapied and Lavelle, 2003). However, *P. corethrus* has been observed in co-existence with native species in some disturbed sites (Table 2). These observations suggest the absence of competitive exclusion as proposed by Marichal et al. (2010).

The literature about biotic interactions with *P. corethrus* is almost exclusively about earthworm/earthworm and plant/earthworm interactions except for a few studies on nematodes. Information about the interaction between *P. corethrus* and other soil macrofauna species is lacking. For instance, *P. corethrus* has been observed in termite galleries (Gates, 1972) but, to our knowledge, no studies on their interactions have been carried out. Moreover, almost no data exist on parasites, pathogens and predators of this species, though such information could improve our understanding of *P. corethrus* invasiveness.

4.2. Evidence of cryptic diversity?

Moreno (2004) mentioned the possibility that studies interested in *P. corethrus* could have mistakenly studied other species in the same genus. Although several complexes of cryptic species have been recently described in earthworms, highlighting the difficulties of morphological diagnosis in this taxon (King et al., 2008; Novo et al., 2010; Pérez-Losada et al., 2009; Shekhovtsov et al., 2016), there is not much data available in the literature on the genetic diversity within the *P. corethrus* morphospecies (Cunha et al., 2014; Dupont et al., 2012). In three populations of *P. corethrus* in the Azores archipelago, Cunha et al. (2014) revealed the existence of two genetically divergent lineages which were morphologically indistinguishable. They showed that one of the lineages was able to cope with the extreme conditions found in the caldera of a volcano where it tolerates a mixture of non-anthropogenic chemical and physical stressors. This lineage could correspond to a new species and, in this case, the adaptation to the caldera environmental conditions cannot be interpreted as the sign of plasticity of *P. corethrus* but instead as the result of a speciation process. This example illustrates that cryptic species may be different in their biological and ecological features and preferences (Birky et al., 2010). Thus, it is conceivable that the variable impacts of *P. corethrus* on the environment, such as its compacting and de-compacting effects,

are evidence of two different species. In this particular case, it seems however that opposite effects are most likely due to soil characteristics. Diaz Cosin et al. (2011) highlighted that comparing published data dealing with species belonging to a complex of cryptic species is dangerous, as the authors could have incorrectly identified the species. They recommended that authors deposit the individuals used in the experiments into a collection in order to eliminate this uncertainty.

By comparing *P. corethrurus* description in different published papers (Table 1), some morphological variability was observed. Further studies are now needed in order to determine if this variability could be explained by the existence of several cryptic species (e.g., James et al., 2010). To test this hypothesis, the concordance between morphological and phylogenetic identification of *P. corethrurus* should be tested in samples coming from its whole distribution range. Moreover, investigations of the reproduction mode and ploidy level of the different lineages would help to test two alternative hypotheses concerning the observation of sexual characters in some *P. corethrurus* specimens: (i) some populations may be mixture of sexual and asexual lineages and (ii) a unique lineage may have a mixed reproductive strategy allowing shifts from sexual to parthenogenetic reproduction according to the environmental conditions.

5. Conclusion

P. corethrurus is the most common and most studied tropical earthworm morphospecies; this review integrated both the most recent and earliest information on its biology and what makes it a successful invader. Its impacts on the environment and other soil organisms were found to be strongly influenced by soil characteristics as well as land use and management. Most of the studies that have been reviewed here have sampled the specimens in the introduced range of the species. Although in some parts of the world this morphospecies has probably reached the integration stage of the invasion process and has established strong biological interaction within ecosystems, in its more recently introduced ranges, *P. corethrurus* populations may not have reached this stage yet. Thus, throughout its distribution area and given the stage of the invasion process that has been reached, population dynamics may be different and studies of ecological processes may not be comparable.

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