Rapid functional response tests for assessing impacts of alien snails on food crops

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Several invasive alien snails are considered a threat to agriculture and horticulture. The development of rapid methods for reliable prediction of their impacts on crops is a major challenge in agricultural science and invasion biology. The use of comparative functional response tests could give insight in the potential impact of alien herbivorous snails on agricultural crops and natural vegetation. It has been hypothesised that invasive alien snails are superior competitors for resources in comparison with common native species, due to higher attack rates and lower handling times of their food. Applications of the functional response approach to terrestrial snails are scarce, despite offering a convenient test design and delivering meaningful mechanistic understanding of resource use of species. The main objectives of this study were (i) to determine the potential grazing effect of the common garden snail \textit{(Cornu aspersum)} on some common agricultural crops, using the functional response approach, (ii) to determine whether the presence of an intraspecific and interspecific competitor affects food consumption of this species, and (iii) to assess the interspecific variation in impact for standardization of functional response tests for herbivorous snails. Food consumption of \textit{C. aspersum} differed significantly for three crops: lettuce (\textit{Lactuca sativa}), endive (\textit{Cichorium endivia var. latifolia}) and common corn salad (\textit{Valerianella locusta}). The functional responses for consumption of \textit{Lactuca sativa} differed significantly between individuals collected from wild and from cultured populations of \textit{C. aspersum}. Furthermore, the food consumption (in dry weight) of \textit{C. aspersum} differed between tests with presence of an intraspecific and interspecific competitor (i.e., \textit{C. aspersum} and \textit{Cepaea nemoralis}, respectively). So, the interspecific and intraspecific competition for resources should be considered in risk assessments in order to generate more reliable impact predictions of alien snail species and to improve our understanding of their interactions with other grazers.

1. Introduction

Species are moved by various human activities beyond the borders of their native geographical ranges (Blackburn et al., 2014). Once introduced, invasive alien species can affect native species and alter the biodiversity (Sala et al., 2000), which can cause severe economic impacts such as damage or loss of food crops (Born et al., 2005). The threat of invasive alien species is expected to increase with increasing globalization of trade and transport (Hulme, 2009; Paini et al., 2016).

A well-known example of an invasive alien species is the brown garden snail \textit{Cornu aspersum} (Müller, 1774). This Mediterranean species is one of the most widely distributed herbivorous snails in the world and is considered an agricultural and garden pest outside its native range (CABI, 2018). The species has been introduced to North and South America, Africa, Oceania, Asia and Northern Europe due to human activities (Guiller et al., 2012; CABI, 2018). These introductions occurred (i) intentionally as food source and as pets; (ii) accidentally by the import of plants and vegetables or transport as hitchhiker on vehicles (Leuven and Van der Velde, 2010; Guiller et al., 2012; CABI, 2018).

\textit{Cornu aspersum} can cause severe damage to food crops and horticultural plants (Guiller et al., 2012). However, this species can also pose a threat to biodiversity and functioning of ecosystems by: (i) selective feeding, which can modify the structure of plant communities (Linhart and Thompson, 1995); (ii) substantial deposit of mucus and faecal material, leading to increasing bacterial and fungal biomass, and hence increased decomposition rates (Theenhaus and Scheu, 1996); (iii) introduction of new parasites associated with snails, which could infect indigenous species (Cabaret et al., 1988; Segade et al., 2013); and (iv)...
acting as a new food source for predators (Peschel et al., 1996; Madec et al., 2000). Its success in colonizing new areas after establishment may be due to: (i) large phenotypic plasticity of various life-history traits (Iglesias and Castillejo, 1999; Madec et al., 2000), and (ii) resistance against natural enemies (Peschel et al., 1996; Madec et al., 2000).

Terrestrial herbivorous snails, such as *C. aspersum*, can consume a wide variety of plant species and detritus and adjust their diet to the food availability (Iglesias and Castillejo, 1999). This capability might determine the wide geographical distribution of these species. Yet, several species do show preference for consumption for certain type of food sources (Williamson and Cameron, 1976; Iglesias and Castillejo, 1999; Chevalier et al., 2003).

A common approach to measure consumption is to compare the quantity of one food item ingested by the consumer in relation to other food using choice tests (Vadas, 1977; Iglesias and Castillejo, 1999). Another method to determine food consumption is the functional response approach (Real, 1977; Xu et al., 2016a). The functional response describes the relationship between resource quantity and resource consumption rate (Holling, 1959; Xu et al., 2016b). In other words, the increase in ingestion rates in response to increasing food quantity as defined by Holling (1959). Three types of functional responses exist: Type I assumes a linear increase in intake with food quantity, type II follows the assumption that the consumer is limited by its capacity to process food, and type III resembles type II, only saturation occurs (Holling, 1959). In general, invasive species consume resources rapidly and more efficiently than native species (Funk and Vitousek, 2007; Morrison and Hay, 2011; Dick et al., 2014). This increases the sensitivity of resources towards potentially severe declines or extinctions (Clavero and García-Berthou, 2005; Salo et al., 2007; Dick et al., 2014). The development of methodologies that predict the potential impact of alien species is a major challenge in invasion biology and pest control (Alexander et al., 2014). Functional responses are important and powerful quantitative descriptions of consumer effects on resources (Vonesh et al., 2017). The use of comparative functional response tests of alien herbivorous snail species could give insight in their potential ecological impact (Dick et al., 2017).

Several studies on predators have already shown that higher functional responses of invasive alien species compared to native species predict actual invader influences in the field (Dick et al., 2013; Alexander et al., 2014). The functional response approach has increasingly been used to predict the ecological impacts of alien predators (Dick et al., 2013; Alexander et al., 2014). Xu et al. (2016b) has already extended this approach to predict the potential impact of herbivorous aquatic snails. However, it is scarcely applied for herbivorous terrestrial snails, despite convenient experimental design and meaningful mechanistic understanding of resource consumption of alien species (Hoxha et al., 2019).

Resource competition is thought to play a major role in resource use within natural population (Svanbäck and Bolinck, 2007). Therefore, intraspecific and interspecific competition between native and invasive species should be included in predictions of ecological and economic impacts of invaders (Violette et al., 2012; Billiard et al., 2016). There is much potential for the use of comparative functional response tests for assessment of interaction between invasive and native species (Mofu et al., 2019).

The main objectives of this study are (i) to determine the potential grazing effect of *C. aspersum* on some common agricultural crops, using the functional response approach, (ii) to determine whether presence of an intraspecific and interspecific competitor affects food consumption of this species, (iii) to assess the interspecific variation in impact to standardize the functional response tests for herbivorous snails. The functional response tests were performed with individuals originating from wild and cultivated populations of *C. aspersum* feeding on three common cultivated plant species: lettuce (*Lactuca sativa* (Linnaeus, 1758)), en-dive (*Cichorium endivia var. latifolia* (Linnaeus, 1758)) and common corn salad (*Valerianella locusta* (Linnaeus, 1758)).

### 2. Materials and methods

#### 2.1. Study organisms and test conditions

Individuals of the common garden snail *Cornu aspersum* and the brown-lipped snail (*Cepaea nemoralis* (Linnaeus, 1758)) were collected in several urban gardens where no molluscicides were used in the municipality Nijmegen (the Netherlands) over the period September and October 2017. In addition, *C. aspersum* was also obtained from a commercial snail farm in the municipality Nieuwlaa, the Netherlands (Slow Escargots, [https://www.slowescargots.nl/](https://www.slowescargots.nl/)). Snails were maintained on a diet of lettuce (*Lactuca sativa*), common corn salad (*Valerianella locusta*), and endive (*Cichorium endivia*) to standardize prior feeding experience to prevent associative learning towards one kind of food source. All organisms were housed in controlled climate facilities and all tests were performed under similar conditions (14 h day/10 h night period, 16 °C, humidity of 72%).

Both test species (*C. aspersum* and *C. nemoralis*) are relatively large-sized land snails with an external shell. Both species are hermaphro-dite. *Cepaea nemoralis* is one of the best-known snail species in Western Europe, mainly because of its polymorphism and bright colours and use in citizen science projects (Silvertown et al., 2011; Kerstes et al., 2019). This snail species was selected because it has overlapping dietary requirements with *C. aspersum* (Williamson and Cameron, 1976; Iglesias and Castillejo, 1999).

#### 2.2. Functional response tests

Three functional response tests were performed to get insight in food consumption of *C. aspersum* (Table 1). Comparison between individuals originating from cultured and wild populations was an additional aim of test 1 and 2. Prior to the tests, snails were held without food for 24 h to allow for standardization of hunger levels, a common method in comparative functional response analyses (Alexander et al., 2014; Xu et al., 2016b). Soil, debris, invertebrates and dead foliage were manually removed from plant material using a paper towel. The plant material for a functional response test was always standardized by similar shape, i.e. cut in rectangular pieces, and weight. Only leaves were used. Fresh leave fragments were blotted with a paper towel and weighted to the nearest 0.1 mg for each food quantity, i.e. 0.5; 1; 2; 4; 6; 8; 10 g (WM0) (Table 1).

### Table 1 Overview of functional response tests with terrestrial snail and plant species.

| Test | Aim | Origin of snails | Food source | Food quantities (g) | Number of individuals |
|------|-----|------------------|-------------|--------------------|----------------------|
| 1.1  | Food consumption and comparison between individuals of cultured and wild populations | Wild and cultured *Cichorium endivia var. latifolia* | 0.5; 1; 2; 4; 6; 8; 10 | For each food quantity: n − 7 + 3 controls |
| 1.2  | Food consumption and comparison between individuals of cultured and wild populations | Wild and cultured *Lactuca sativa* | 0.5; 1; 2; 4; 6; 8; 10 | For each food quantity: n − 7 + 3 controls |
| 1.3  | Food consumption | Cultured *Valerianella locusta* | 0.5; 1; 2; 4; 6; 8; 10 | For each food quantity: n − 7 + 3 controls |
The weighted leave fragments were then distributed in plastic cups (diameter 9.5 cm, height 10.5 cm). Snails were weighted before each test and only one snail was added to each cup. Three control cups only contained plant material and were kept grazer-free. During the 48 h test period, consumed plant material was not replaced. At the end of the test, the remaining plant material was blotted with paper towel and weighted again (WM\textsubscript{c}0) to determine the consumption.

The consumption by each snail was subsequently determined by the difference between initial and final wet weight of plant material. The potential plant decomposition or growth during the test was determined by subtracting initial plant biomass from the biomass in control cups after 48 h (M\textsubscript{control 48h} - M\textsubscript{control time zero}) (Xu et al., 2016a). The consumption by snails was then determined by adding net mass consumption (M\textsubscript{treatment time zero} - M\textsubscript{treatment 48h}) to the average potential plant decomposition or growth. Consumption was standardized for weight to plant weight consumed per gram snail. The weight of snails was always measured with their shell. For each food quantity, seven replicates and three controls were used (Table 1).

2.3. Functional response analyses

To establish whether the relationship between plant quantity and the amount of consumed plant material by snails was best described by a Type II or a Type III response, the ‘frair\textsubscript{test}’ function in ‘FRAIR’ package was used (R Core Team, 2016; Pritchard et al., 2017). Type II functional responses were indicated by a significant negative first-order term, whereas a significant positive first-order term followed by significant negative second-order term indicated a Type III functional response (Juliano, 2001; Paterson et al., 2015; Pritchard et al., 2017). All functional responses proved to be a Type II functional response. This type describes the functional responses where the consumed resources are not replaced. Therefore, Rogers’ random equation is used (Eq. (1), Rogers, 1972; McCoy et al., 2012; Barrios-O’Neill et al., 2014; Toscano and Griffen, 2014; Xu et al., 2016a):

\[
N_e = N_0 (1 - \exp(a(N_e - T)))
\]  

Where \(N_e\) is the amount of resource eaten, \(N_0\) is the initial resource quantity, \(T\) is the total test time and \(a\) and \(h\) are the coefficients for attack rate and handling time, respectively. This recursive function can be solved using the Lambert W function (Eq. (2), Corless et al., 1996; Xu et al., 2016a):

\[
N_e = N_0 - \frac{W(a h N_0 \exp(-a^* (T - h N_0)))}{a h}
\]

The parameters ‘\(a\)’ and ‘\(h\)’ for the functional response of each feeding test were estimated using the ‘emdl’ function of the package ‘FRAIR’ in R, which solves the random predator equation using the LambertW equation (R Core Team, 2016; Pritchard et al., 2017). In the context of herbivores, parameters ‘\(a\)’ and ‘\(h\)’ could be interpreted as ingestion rates (the product of bite frequency and bite volume) and as chewing time, respectively (Farnsworth and Illius, 1996; Yearsley et al., 2001; Thompson Hobbs et al., 2003; Xu et al., 2016a).

Subsequently, functional response curves were fit to the data using ‘rogersII’ function of the package ‘FRAIR’ in R and the confidence intervals were compared with the ‘frair\textsubscript{compare}’ function (R Core team, 2016; Pritchard et al., 2017). To visualise variability around the fitted curves, 95% BCa confidence intervals were drawn from bootstrap populations generated from the original data (frair:frair.boot). Based on the output from bootstrapped fits, functional response curve could be constructed using the ‘drawpoly’ function of the package ‘FRAIR’ in R.

2.4. Competition test

Modifications were made to the plastic cups by adding a plastic filter cup with a large mesh size of approximately 3 mm (Fig. 1). The mesh allowed for exchange of mucus and pheromones between both compartments, whereas it limited shared consumption of food resources. The plant species used for this test was \(L.\ sativa\), as this was known to be consumed by both snail species (unpublished results). Fresh plant fragments were blotted with a paper towel and weighted to the nearest 0.1 mg to yield a food quantity of 6 g (WM\textsubscript{c}). In addition, a test was conducted with individual snails in absence of a competitor (Test 2.3). This test was used as reference. Furthermore, this test followed the same test procedure concerning weighing snails, cleaning plants and feeding as the functional response tests of this study.

At the end of the test period, the remaining plant material was blotted with paper towel and weighted again (WM\textsubscript{t}) to determine the consumption by snails. Subsequently, remaining plant fragments were dried in an oven (>48 h at 70 °C) allowing for measuring the remaining dry mass (DM\textsubscript{t}). Dry mass was used to minimize measurement errors due to water and snail slime absorption by plant material (Cronin, Wissing and Lodge, 1998; Elger and Willby, 2003). The initial fresh-to-final dry mass ratio of the plant controls was used to calculate initial dry mass of the plant material (DM\textsubscript{c}) from initial wet mass of the plant material (WM\textsubscript{c}) following Elger and Barrat-Segretain (2004) (Eq. (1), cited in Grutters et al., 2017). Both wet and dried plant consumption by snails was measured as the difference between initial and final wet weight. The potential plant decomposition or growth during the test was determined by subtracting initial plant biomass from the biomass in control cups after 48 h (M\textsubscript{control 48h} - M\textsubscript{control time zero}) (Xu et al., 2016a, 2016b). The consumption by snails was then determined by adding net mass consumption (M\textsubscript{treatment time zero} - M\textsubscript{treatment 48h}) to the average potential plant decomposition or growth. The snails differed in weight; therefore, consumption was given in plant consumed per gram snail (measured including shell).

Snails that where alive but did not show consumption were included in the analysis and assigned a consumption of zero (Baker et al., 2010). Data was checked for normality with Shapiro-Wilk test and post hoc analyses were performed with a Tukey test to compare the different functional response tests (multcomp package R; Hothorn et al., 2016; R Core Team, 2016). For each test, six replicates and three controls were used (Table 2).

3. Results

3.1. Functional response tests

The tests with three different cultivated plant species showed a Type II functional response for food consumption of \(C.\ aspersum\) originating from cultured populations (Fig. 2). There was no overlap in 95% confidence intervals, indicating substantial differences in efficiency and rate
of snail feeding on three plant species. The snails had a significantly greater attack rate \((a = 0.049)\) for \(L.\) sativa than for \(C.\) endivia \((a = 0.023; z = 16.66, P < 0.001)\) and \(V.\) locusta \((a = 0.004; z = 8.19, P < 0.001)\), as well as a significantly shorter handling time \((h = 0.002)\) for \(L.\) sativa than for \(C.\) endivia \((h = 0.004; z = -7.96, P < 0.001)\) and \(V.\) locusta \((h = 0.031; z = -8.40, P < 0.001)\) (Fig. 2, Table A3).

Individuals of \(C.\) aspersum originating from wild populations also showed a Type II functional response (Fig. 3). There was an overlap in 95% confidence intervals and intersect, indicating an overlapping feeding efficiency and rate between individuals originating from wild and cultured populations. Individuals originating from wild populations had a significantly greater attack rate when feeding on \(L.\) sativa \((a = 0.291)\) than individuals originating from the cultured population \((a = 0.049; z = 17.60, P < 0.001)\), but a significantly longer handling time \((h = 0.006 \text{ versus } h = 0.002; z = 34.69, P < 0.001)\) (Fig. 3B, Table A4).

When feeding on \(C.\) endivia, individuals originating from wild populations had a significantly greater attack rate \((a = 0.072)\) than individuals originating from the cultured population as well \((a = 0.023; z = 18.98, P < 0.001)\), but a similar handling time \((h = 0.004 \text{ versus } h = 0.004; z = -0.77, P = 0.441)\) (Fig. 3B, Table A4).

### 3.2. Competition test

The competition test demonstrated that the feeding activity of \(C.\) aspersum differed between tests with and without another snail in the same cup (Fig. 4). The consumption of the grazer was higher than the reference consumption when the competitor had access to a food source and lower when the other snail had no access to a food source (Fig. 4). Post-hoc analyses indicated that this finding was significant when the competitor was \(C.\) nemoralis (Table A5).

### 4. Discussion

Many studies use the functional response approach as a tool for predicting the ecological impacts of invasive species on the recipient communities (Xu et al., 2016a, 2016b; Dick et al., 2017; Hoxha et al., 2019; Mofu et al., 2019). This study is the first assessment of the functional response for plant consumption by \(C.\) aspersum. The consumption of \(C.\) aspersum differed significantly for three crops and between individuals of wild and cultured populations. Furthermore, the food consumption of \(C.\) aspersum differed between tests with and without presence of an interspecific competitor.

The functional response approach with herbivorous snail species comprises some uncertainties. The mucus of snails could soak the plant material, resulting in an increase in wet weight of the remaining plant material. This process may cause an underestimation of consumption rates and therefore an underestimation of the functional response. Tests with snails in the same cup as the plant material but without the possibility to consume the plant material could validate this assumption. The findings in the competition test underpins this ‘soaking effect’. However, the use of dry weight instead of wet weight could also cause uncertainty because the dry weight of the plant material at the start of this test was estimated using the wet/dry weight ratio of the controls. For freshly consumed vegetables, it seems more valuable to get insight in effects of grazing on wet weight loses of crops, as this measurement is more relevant for commercial farmers and economic markets than dry weight of crops. Crop damage can result in lost production, diminished quality and increased production costs. Data on consumed wet weight by invasive snails is also useful for quantification of these figures (Pimentel et al., 2005; Paini et al., 2016).

Another reason for the differences in functional response could be...
variability in palatability of plant material, due to the limitation of not being able to conduct all tests at the same time. Tests were performed in various periods. Plant material could seasonally differ in quality and thereby causing variation in consumption rate of snails. Moreover, (seasonal) differences in the use of pesticides during agriculture could have an effect on palatability of vegetables by snails (Barker and Watts, 2002). This could cause bias in the outcome of the tests. Crops originating from agriculture that used other or no pesticide could be more palatable than our study showed. The pesticide used in the crops of this study are for instance abamectin and delamethrin (Natuur and Milieu et al., 2017). However, in the future the use of pesticide will be less, which will increase the palatability of the crops for snails. Furthermore, associative learning and post-ingestive effects may affect food selection and consumption rate of snails (Gelperin, 1975; Chevalier et al., 2003). Teyke (1995) showed that an appetitive learning modifies foraging behaviour of a generalist herbivorous snail. In other words, after consuming a particular food, the snails in subsequent foraging excursions move directly towards the particular food and consume it (Peschel et al., 1996). This illustrates that origin of food and test animals should be taken into account in comparative functional response analyses and generalizations of outcomes to field situations. For further research, nutritional traits of the food source could be determined to indicate the differences in consumption of the tested individuals.

Mostly, individuals from wild populations of snail species will occur in the farmer’s field. However, escapes and intentional introductions of individuals from cultured populations in snail farms may also be pathways for spread of invasive snails. According to the findings in this study, functional responses of C. aspersum originating from wild populations significantly differ from those originating from cultured populations when feeding on endive and lettuce. This highlights the caution in which the outcome of functional response tests should be treated as it can lead to an overestimation or underestimation of the functional response. There are several possible explanations for the difference in functional response observed between both populations such as species plasticity or breeding control by the snail farmer (Madec and Daguzan, 1993; Dupont-Nivet et al., 1997). The conditions of a snail farm are for instance ‘optimal’ as the wild populations live under unpredictable ‘harmful’ conditions. It is possible that individuals originating from cultured populations will adapt to their new environment, in which there could be no significant difference between individuals originating from cultured populations and individuals from wild populations. However, it is also of value to identify whether individuals from wild and cultured populations differ in feeding behaviour and (harmful) effects during the early invasion phase. A long-term experiment should be conducted to get more insight in these aspects during the late establishment phase. Spatial and temporal heterogeneity in the range of

**Fig. 3.** Functional response curves for consumption of Lactuca sativa (a) and Cichorium endivia (b) by Cornu aspersum originating from cultured and wild populations. Consumption is modelled as weight of the plant using the Roger’s random predator equation for a Type II response (n = 7 snails per plant quantity; shaded areas are bootstrapped 95% confidence intervals).
C. aspersum species are associated with a large phenotypic variation in combinations of life-history traits, especially reflecting a high degree of plasticity (Madec and Daguzan, 1993). This plasticity may be key to the colonization success of C. aspersum habitats involving frequent extinction-recolonization processes (intensive agricultural zones), when C. nemoralis are unable to make such colonization, despite frequent sympathy in other environments and closely related dispersal strategies (Oosterhoff, 1977; Madec et al., 2000).

Interaction between individuals is already taken into account in some functional response studies (Mofu et al., 2019). Inter- and intraspecific interaction is central in most ecological processes (Billiard et al., 2007). Resource competition is thought to play a major role in resource use within natural populations (Svanbäck and Bolnick, 2007). The findings of the competition tests show interspecific resource competition between C. aspersum and C. nemoralis, and intraspecific competition for C. aspersum. The food consumption variations found in presence of another snail, with or without a food source, could be caused by some kind of interaction between the individuals. Perhaps excretion of pheromones or different types of snail slime could play a role in these findings (Dan and Bailey, 1982; Shaheen et al., 2005). Dan and Bailey (1982) showed that interaction between C. aspersum and C. nemoralis resulted in an inhibition effect on the activity of C. aspersum. This is in line with the findings of less plant consumption by C. aspersum in the presence of another individual that has no access to food. However, the consumption rate increases when the other snail has access to lettuce. These results highlight that interspecific and intraspecific variation on feeding behaviour should be taken into account in future research because it can affect the functional response of snail species and may cause overestimations as well as underestimations of their invasiveness. For further research, more snails in one test area or mixing the excretion of various snails during the competition test could give insight in the possible bias created by the effect of individual behaviour of the snails.

According to the aforementioned method-uncertainties, the use of functional response tests should be standardized with a protocol to minimalize variation between outcomes when used as a potential risk predictor in decision-making. Nevertheless, the functional response approach is valuable for assessing potential impacts of invasive species owing to its relative ease of derivation and its applicability for testing any organism’s utilization of resources (Funk and Vitousek, 2007; Dick et al., 2014).

Despite some uncertainties, the functional responses of C. aspersum are useful for predictions of their ecological and agricultural impact in comparison with native herbivorous (snail) species. C. aspersum is considered an agricultural and garden pest outside its native range (CABI, 2018).

According to the findings in this study, C. aspersum is capable to consume well-known crops, such as lettuce (L. sativa), endive (C. endivia) and corn salad (V. locusta). The consumption of L. sativa by C. aspersum is significantly higher than that of the other crops, which indicates that farmlands with L. sativa will have potentially more crop damages by this invasive snail species than farmlands with C. endive or V. locusta. As these three crops are common grown, the predicted crop damage by C. aspersum could potentially lead to an increase in crop protection measures such as chemical or biological control of snails. These measures can also have an effect broader than on just the target organisms. Therefore, early insight in the potential risk of invasive alien species for various crops and rapid responses will be required to minimize their economic as well as environmental impact. Standardized functional response tests will facilitate rapid impact assessments of introduced herbivorous species for a broad spectrum of crops and environmental conditions in farmlands.

**CRedit authorship contribution statement**

N.W. Thunnissen: Formal analysis. F.P.L. Collas: Conceptualization. R.S.E.W. Leuven: Supervision, Conceptualization.

**Declaration of Competing Interest**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

**Appendix A. Supplementary data**

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2020.107138.
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