To stay or to go: Resource diversity alters the dispersal behavior of sympatric cryptic marine nematodes

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ABSTRACT

Animals can display informed dispersal strategies, wherein individuals use specific environmental cues to decide whether and where to disperse. Patch conditions are known to affect the dispersal behaviour of organisms, but empirical studies investigating the impact of resource diversity on the dispersal of closely related species are largely lacking. Here, we investigated the effects of food diversity on the dispersal of three co-occuring cryptic species of the marine nematode complex *Litoditis marina* (Pm I, Pm III and Pm IV) using microcosms consisting of a local patch (*i.e.*, inoculation plate), connection tube, and distant patch (*i.e.*, dispersal plate). The patches had either identical food treatments ('homogeneous patches'), or with *Escherichia coli* in the local patches and more diverse food (low, medium, or high-diversity food) in distant patches. Our results show that the dispersal behaviour of the cryptic species varies depending on food diversity, indicating that *L. marina* acquire information about their environment when making dispersal decisions. All the cryptic species tend to disperse faster toward food patches that increase nematode fitness. Pm I and Pm IV exhibited faster dispersal towards patches with a more diverse food source, whereas the two most diverse food sources and *Escherichia coli* equally triggered the dispersal of Pm III. This indicates that resource diversity can alter the dispersal behaviour of cryptic species and may be an important mechanism to achieve species coexistence in the field.

INTRODUCTION

Dispersal is a fundamental ecological process that shapes local and regional diversity patterns, with profound effects on population dynamics, species coexistence, and evolutionary outcomes (Leibold and McPeek, 2006; Ronce, 2007; Bonte et al., 2012). It is essential for most animals to escape unfavorable environmental conditions and/or locate suitable food resources for survival and reproduction (Ronce, 2007; Clobert et al., 2009; Urban et al., 2016). Theoretical and empirical studies demonstrate that dispersal is condition-dependent and an informed process (Clobert et al., 2009). The information to disperse can be acquired through a variety of cues, such as local population density (Bowler and Benton, 2005; Matthysen, 2005; Bitume et al., 2014), body condition (Bonte and De La Peña, 2009), or abiotic factors (Altermatt and Ebert, 2010). Food availability can also trigger dispersal, wherein individuals tend to be more dispersive when local resources are scarce (Aguillon and Duckworth, 2015; Fronhofer et al., 2015; Kreuzinger-Janik et al., 2022). Food resources are generally distributed in the environment in patches of different abundances and diversity, but surprisingly little is known on how food diversity influences the dispersal behavior of organisms.

The effects of food diversity in shaping the structure of ecological communities remains a matter for debate (Duffy, 2002). Some theoretical predictions indicate that diverse food sources will be less beneficial for a population of consumers because these are more likely to contain food that is resistant to consumption ('variance-in-edibility hypothesis') (Leibold, 1989; Hillebrand and Shurin, 2005), or because these may reduce both the relative and absolute abundances of the preferred food of consumers ('dilution or resource concentration hypothesis') (Andow, 1991; Joshi et al., 2004; Keesing et al., 2006). Alternatively, a more diverse food source may be advantageous for a population since it can provide a more complete range of nutritional resources for the consumers ('balanced-diet hypothesis') (DeMott, 1998; Pfisterer et al., 2003; Worm et al., 2006) and/or may enhance dietary specialization because of greater foraging possibilities (Araújo et al., 2011; Bolnick et al., 2011).

Despite the significance of food diversity in population dynamics, empirical studies investigating its impact on dispersal and species coexistence are largely lacking. The link between diet and dispersal has often been studied in the framework of optimal foraging theory, which broadly predicts that individuals adaptively alter their diet or behavior depending on environmental conditions (MacArthur and Pianka, 1966; Stephens and Krebs, 1986). Ideally, individuals should make fully informed dispersal decisions based on the conditions of the local and distant patches (Clobert et al., 2009). Individuals may assess the quality of a patch through direct exploration or through remote detection of potential food patches by olfactory and visual sensory cues (Bowler and Benton, 2005). Organisms may also estimate the quality of a patch based on evolved expectations of food quality and abundance (Bowler and Benton, 2005), energy intake per unit of foraging effort (Charnov, 1976), and/or contribution to fitness (Mcgraw and Caswell, 1996; Coulson et al., 2006). There is ample evidence showing that animals have different dispersal strategies, and these strategies can even differ between closely related species (Han and Dingemanse, 2015). Such differences in dispersal strategies are likely to evolve due to spatial and temporal variation in patch conditions (McPeek and Holt, 1992; Henriques-Silva et al., 2015). In addition, differences in dispersal behaviour may play an important role on the sympatric co-occurrence of closely related species (Aiken and Navarrete, 2014; Yawata et al., 2014). For instance, by dispersing to different microhabitats or utilizing different resources, closely related species that may have similar ecological requirements can minimize overlap and competition for the same resources. This strategy of niche differentiation can reduce direct competition, which may allow species to coexist within a community (Mittelbach and McGill, 2019; De Meester et al., 2012, 2015a). While previous studies have demonstrated that increased resource diversity may mitigate competition through enhanced niche differentiation (Martin and Garnett, 2013; Sánchez-Hernández et al., 2017), empirical studies on the effects of food diversity on dispersal strategies, and whether these vary between closely related species and contribute to their coexistence, have been rarely carried out.

In this regard, the cryptic species complex *Litoditis marina* represents an excellent candidate for testing whether food diversity can affect the dispersal behavior of sympatric closely related species. *L. marina* is a marine bacterivore nematode complex consisting of co-occurring species that are morphologically (nearly) identical but genetically distinct, which exhibit differences in ecological and functional traits such as life histories (De Meester et al., 2015b), feeding habits (Derycke et al., 2016), and microhabitat preferences (Guden et al., 2018). These cryptic species are associated with living and decomposing macroalgae in intertidal zones (Derycke et al., 2006), a highly dynamic environment where abiotic and biotic conditions rapidly fluctuate both at temporal and spatial scales (Moens and Vincx, 2000a,b). In such heterogeneous environments, dispersal is crucial to avoid unfavourable conditions (Snyder and Chesson, 2003). Differences in dispersal strategies have been observed between the different cryptic species of *L. marina* (De Meester et al., 2012), which can be influenced by competition (De Meester et al., 2015a). While our previous investigations revealed that food diversity can alter the life-history traits and food preferences of the cryptic species (Guden et al., 2021)) and can change the outcomes of intra- and interspecific interactions (Guden et al., 2021, 2024)), the impact of food diversity on active dispersal of *L. marina* remains to be tested.

In the present study, we investigated the dispersal behavior (*i.e.*, time of nematode dispersal and proportion of dispersers) of the three cryptic species of *L. marina* (Pm I, Pm III and Pm IV) in patches with different food treatments (*E. coli*, low-, medium-, and high-diversity food). First, we tested the effects of food diversity on dispersal in homogeneous patches consisting of the same bacterial food treatments in local and distant patches. Traditional models predict that differences in dispersal behaviour between species will be largely dependent on differences in life-history characteristics in a homogeneous landscape where environmental conditions are relatively uniform across the entire area (Amarasekare and Possingham, 2001; Logue et al., 2011). We hypothesized that the differences in active dispersal between the cryptic species of *L. marina* are not only solely explained by differences in their life-history attributes, but also by food diversity. Hence, we expected that the dispersal behaviour of *L. marina* would also vary depending on food diversity. Second, we tested the effects of food diversity on dispersal in heterogeneous patches consisting of *E. coli* in the local patches and different levels of food diversity in the distant patches. Since *L. marina* generally exhibit higher fitness on a more diverse food source (Guden et al., 2021), we hypothesized that a more diverse food in distant patches would trigger faster nematode dispersal. Investigating the effects of food diversity on the dispersal behavior of cryptic species can shed light on the evolution of feeding adaptations in closely related species, and is needed to deepen our understanding on community dynamics and species coexistence.

METHODS

Nematode cultures

Monospecific cultures of three cryptic species of *Litoditis marina* (Pm I, Pm III, and Pm IV) were initially established from individual gravid females collected in the field. Pm I and Pm III originated from the Paulina salt marsh in the Schelde Estuary, The Netherlands (51° 21’ N, 3° 49’ E), while Pm IV was obtained from Lake Grevelingen, a brackish-water lake in The Netherlands (51° 44’ N, 3° 57’ E). The nematodes were allowed to reproduce for multiple generations to create stock cultures, which were maintained in the dark under standardized conditions (salinity of 25 temperature of 20°C). Nematodes used in the experiments were harvested from the nematode stock cultures in exponential growth phase.

Food sources for nematodes

To investigate the effects of food diversity on active dispersal behavior of the different cryptic species of *L. marina*, we selected and prepared bacterial food sources according to the protocol described by Guden et al. (2021). Briefly, twenty-five marine bacterial strains were selected as bacterial food sources for the nematodes because they were among the most abundant bacterial taxa found in the microbiome *sensu lato* of specimens of at least one cryptic species of *L. marina* collected from the field (Derycke et al., 2016). After preparing monospecific liquid cultures of these twenty-five marine bacterial strains, the bacterial suspensions of each bacterial strain were diluted to approximately 3×10^9 cells ml^{-1}, a density known to support active population growth and good individual fitness of *L. marina* (dos Santos et al., 2008; De Meester et al., 2011; Guden et al., 2021).

Our experiments consisted of three resource-diversity treatments: ‘low-diversity food’, ‘medium-diversity food, and ‘high-diversity food’. These treatments were prepared by mixing culture aliquots of bacterial strains, as described by Guden et al. (2021). Low-, medium- and high-diversity food treatments consisted of 5, 10, and 15 bacterial strains, respectively. For each food-diversity treatment, the component bacteria were mixed to attain approximately equal cell numbers of all bacterial strains, with a final density of approximately 3 × 10^9 cells ml^{-1}. Because we were interested in investigating the effects of food diversity on the dispersal of the cryptic species, the replicates in each food-diversity treatment consisted of bacteria that were chosen at random from our pool of twenty-five bacterial strains. Frozen-and-thawed *Escherichia coli* (strain K12, density of ca. 3 × 10^9 cells ml^{-1}) was used as a control food treatment, which is a suitable food source that has been used in previous culture experiments with *L. marina* (Moens and Vincx, 1998; dos Santos et al., 2008; De Meester et al., 2011).

Experimental design

A summary of the experimental design is presented in Fig. 1. The time of first effective dispersal, *i.e.*, dispersal followed by emergence of active juveniles in the distant patch regardless of whether the individual was already gravid before the dispersal event, was used to measure the dispersal rates of *L. marina* (De Meester et al., 2012). The time of first effective dispersal is henceforth referred to as ‘time of dispersal’, and implies that the longer the time of dispersal, the slower the dispersal rate of the nematodes. To investigate the effects of food diversity on the time of dispersal of the cryptic species of *L. marina*, we used specially designed dispersal plates consisting of two Petri plates (resp. ‘local’ and ‘distant’ patches, 5 cm i.d.) connected by a tube (1 cm i.d. and 10 cm length) (Fig. 1A) (De Meester et al., 2012). The substratum in the plates was provided as 60 ml of a 1.5% bacto agar medium prepared with ASW (salinity of 25, pH of 7.5–8), with additional cholesterol (100 μl^{-1}) as a source of sterols. The agar medium was spread to a perfectly plain level across both plates and connecting tube.

Using the different food-diversity treatments (Fig. 1B), we performed two experimental setups with homogeneous and heterogeneous food patches to assess the effects of food diversity on active dispersal behavior of *L. marina*. Homogeneous patches consisted of the same bacterial treatments both in the local and distant patches. Heterogeneous patches consisted of *E. coli* as bacterial food treatment in the local patch, and with a diverse food treatment in the distant patch to test whether food diversity can trigger dispersal. All three cryptic species of *L. marina* were used in the ’heterogeneous’ setup, whereas only Pm I and Pm III were used in the ’homogeneous’ set-up due to time constraints since all the experiments had to be started at the same time. In addition, Pm I and Pm III showed distinct dispersal abilities based on previous investigation

(De Meester et al., 2012, 2015a), which makes them particularly interesting in testing whether resource diversity influences active dispersal.

To investigate the effects of food diversity on the dispersal behaviour of *L. marina* (Pm I and Pm III) in homogeneous patches, 50-µl suspensions of the same bacterial food treatments were added both in the local and distant patches. The E-E, L-L, M-M, and H-H treatments consisted of *E. coli*, low, medium and high-diversity food in both patches, respectively (Fig. 1C). The treatment with *E. coli* in local and distant patches (‘E-E’) was used as a control. In heterogeneous patches, we investigated whether food diversity is an important driver for the dispersal of the cryptic species (Pm I, Pm III and Pm IV) by adding 50-µl suspensions of a single-strain resource (*E. coli* K12) in local patches, and an equal amount of bacterial suspensions of low-, medium-, or high-diversity food in the distant patches (henceforth referred to as ‘E-L’, ‘E-M’, and ‘E-H’ treatments, respectively) (Fig. 1D). The treatment with *E. coli* in both patches (‘E-E’) was also used here as a control.

After adding food to the patches, five adult males and five adult females of a single species were manually picked from the stock cultures and transferred randomly to the local patches at the beginning of the experiment. No nematodes were added to the distant patches. Food was replenished in both the local and distant patches every five days to minimize changes to the food-diversity gradient. Using the same preparation of bacterial mixture as food for nematodes, our previous experiments demonstrated a food-diversity effect on the population growth of *L. marina* within a week (Guden et al., 2021, 2024), supporting the persistence of diversity gradients in the food treatments for at least five days. All microcosms were incubated in the dark at a constant temperature of 20°C, with four independent replicates per food treatment for each cryptic species. The numbers of nematodes in the distant patch were counted daily to check for dispersers. The timing of the arrival of the nematode(s) in the distant patches was recorded as the ’time of dispersal’ when it was followed by reproduction (i.e., time of first effective dispersal). In all setups, the numbers of adult nematodes in the local patches at the time of dispersal were also counted to determine the proportion of nematodes that dispersed. The proportion of dispersers was calculated by counting the number of adult nematodes in the distant patch and dividing it by the total number of adult nematodes both in the local and distant patches at the time of dispersal.

Data analyses

Differences in time of dispersal and proportion of dispersers between different food treatments were tested in R (R Core Team, 2024). All analyses were conducted with the data of adult nematodes only since it was not feasible to differentiate real juvenile dispersers and offspring of dispersed adults. Parametric tests (ANOVA) were used after checking for normality and/or homoscedasticity using the Shapiro-Wilk test and Levene’s test, respectively. Posterior pairwise comparisons were performed using a post-hoc Tukey Honest Significant Differences (HSD) test.

Food diversity effects on the dispersal of L. marina in homogeneous patches

To test for differences in dispersal rates between food treatments in homogeneous patches, a one-way ANOVA test was performed on the time of dispersal as the dependent variable and with food diversity (4 levels: E-E, L-L, M-M, and H-H) as the fixed factor for each cryptic species (Pm I and Pm III). A one-way ANOVA, with the same fixed factor, was also performed to test for differences in the proportion of nematode dispersers. To test whether the proportion of dispersers was correlated with the time of dispersal, Pearson correlation coefficients were calculated for each species, and p-values were corrected for multiple testing with the Bonferroni method.

Food diversity effects on the dispersal of L. marina in heterogeneous patches

To test whether food diversity can trigger the dispersal of the cryptic species of *L. marina*, we assessed differences in the time of dispersal in the setup with heterogeneous patches. A one-way ANOVA test was performed on the time of dispersal as the dependent variable and with food diversity (4 levels: E-E, E-L, E-M, and E-H) as the fixed factor for each cryptic species (Pm I, Pm III and Pm IV). A separate one-way ANOVA test was also performed to test for differences in the proportion of nematode dispersers, with the same fixed factor. Pearson correlation coefficients were calculated for each species to test whether the proportion of dispersers was correlated with the time of dispersal, with Bonferroni correction for p-values.

RESULTS

Food diversity effects on nematode dispersal in homogeneous patches

In homogeneous patches with the same food treatments in local and distant patches, food diversity showed a significant effect on the time of dispersal of Pm I (all $p<0.0001$) and Pm III ($p < 0.005$) (Table 1; Fig. 2). Among all food treatments, Pm I showed the fastest dispersal in the treatment with high-diversity food (H-H), while it exhibited the slowest dispersal with *E. coli* (E-E) (all $p<0.05$) (Table 2). In Pm III, we observed significantly slower dispersal in the treatment with low-diversity food (L-L) compared to *E. coli* (E-E) ($p < 0.05$) and high-diversity food (H-H) ($p < 0.005$), but no significant differences were found between other food treatments (all $p>0.05$). Food diversity also had a significant effect on the proportion of nematodes that dispersed on the time of dispersal for Pm I ($p < 0.0001$) and Pm III ($p < 0.005$) in homogeneous patches (Table 1; Fig. 2). Pm I showed higher proportion of dispersers in the two most diverse food treatments (M-M and H-H) compared to the other treatments, while the lowest proportion of dispersing nematodes was observed when both local and distant patches had *E. coli* (all $p<0.01$) (Table 3). In contrast, Pm III had the highest proportion of dispersers in the treatment with low-diversity food (L-L), and had significantly lower proportion of dispersers in the treatment with *E. coli*

(E-E) and medium-diversity food (M-M) compared to other treatments (all $p<0.05$). Pearson's correlation analysis revealed that the proportion of nematodes that dispersed was significantly negatively correlated with the time of dispersal of Pm I (Pearson's correlation = -0.80, $p<0.001$) in homogeneous patches, but no significant correlation was found in Pm III ($p>0.05$).

Food diversity effects on nematode dispersal in heterogeneous patches

In heterogeneous patches with single-strain resource *E. coli* in the local patches and different food-diversity treatments in the distant patches, we observed a significant effect of food diversity on the time of dispersal of Pm I, Pm III and Pm IV (all $p<0.001$) (Table 1; Fig. 3). Pm I exhibited the fastest dispersal toward distant patches with high-diversity food (E-H) among all food treatments (all $p<0.05$), and the slowest dispersal toward distant patches with *E. coli* (E-E) (all $p<0.0001$) (Table 2). In contrast, Pm III exhibited the slowest dispersal toward distant patches with low-diversity food (E-L) (all $p<0.05$), but no significant differences in dispersal rates were observed between other food treatments (all $p>0.05$). In Pm IV, faster dispersal was observed toward distant patches with medium- and high-diversity food compared to other treatments (all $p<0.05$), and the slowest dispersal toward distant patches with *E. coli* (all $p<0.01$).

In addition, food diversity had a significant effect on the proportion of nematode dispersers for Pm I ($p < 0.0001$), Pm III ($p < 0.001$) and Pm IV ($p < 0.001$) in heterogeneous patches (Table 1; Fig. 3). Pm I showed the highest proportion of dispersers toward high-diversity food (E-H) among all food treatments, and the lowest proportion of dispersers toward *E. coli* (all $p<0.05$)(Table 3). Pm III exhibited significantly lower proportion of dispersers toward distant patches with low-diversity food (all $p<0.05$), but no significant differences were found between other treatments (all $p>0.05$). In Pm IV, we observed significantly higher proportion of dispersers toward distant patches with medium- and high-diversity food compared to other treatments, and the lowest proportion of dispersers toward distant patches with *E. coli* (all $p<0.05$). Pearson's correlation analysis revealed that the proportion of nematodes that dispersed was significantly negatively correlated with the time of dispersal of Pm I (Pearson's correlation = -0.78, $p<0.001$), Pm III (Pearson's correlation = -0.59, $p<0.05$), and Pm IV (Pearson's correlation = -0.73, $p<0.005$) in heterogeneous patches.

DISCUSSION

Although dispersal is known to play an important role in species coexistence, the impact of food diversity on the dispersal behaviour of co-occurring closely related species remains largely unexplored. Using the cryptic nematode species complex *Litoditis marina* as a model system, the present study provides empirical evidence that food diversity can alter the dispersal behavior of cryptic species. A summary of the results can be found in Table 4.

In a homogeneous landscape where environmental conditions (e.g., habitat quality, resource availability, and climate) are relatively uniform across the entire area, traditional models predict that differences in dispersal behaviour will be largely dependent on the life-history characteristics of species (Amarasekare and Possingham, 2001; Logue et al., 2011). In our experiment with homogeneous conditions consisting of *E. coli* as food (E-E) both in local and distant patches, we observed slow dispersal of Pm I (ca. 15 days) but fast dispersal of Pm III (ca. 4 days) (Fig. 2), in agreement with De Meester et al. (2012). Pm I and Pm III differ in life-history traits such as reproductive strategy, fecundity and population growth, but these differences are rather subtle and vary depending on environmental conditions (De Meester et al., 2015b; Guden et al., 2021, 2024). If the differences in active dispersal between the cryptic species of *L. marina* are solely explained by differences in their life-history attributes, we would expect Pm III to consistently exhibit faster dispersal than Pm I regardless of the diversity of food in the patches. Conversely, we observed variation in nematode dispersal depending on food diversity. Pm I exhibited the fastest dispersal to patches with high-diversity food (H-H) among all food treatments, which coincided with the high proportion of nematode dispersers. In contrast, homogeneous patches with *E. coli* (E-E), medium-diversity food (M-M), and high-diversity food (H-H) equally triggered fast dispersal of Pm III. Such dispersal behaviour was likely not driven by population density since both Pm I and Pm III started to disperse even at low numbers of nematodes in the local patch at the time of dispersal (Supplementary material, Fig. 1). The differences in the dispersal behaviour of the cryptic species in response to food diversity, may, however, be related to their food preferences, which have been found to be species-specific in *L. marina* and vary depending on food diversity (Guden et al., 2021, 2024).

The important effect of food preferences on the dispersal behaviour of *L. marina* is supported by our findings on nematode dispersal in a heterogeneous condition consisting of *E. coli* as a food source in the local patch and more diverse food in the distant patch (Fig. 3). Here, both Pm I and Pm IV exhibited faster dispersal to distant patches with a more diverse food source than to distant patches with *E. coli* regardless of population density (Supplementary material, Fig. 1), indicating that food diversity mainly drives the dispersal of these cryptic species. Pm IV particularly showed faster dispersal toward the two most diverse food sources among all food-diversity treatments, in accordance with its food preference based on taxis-to-food assays (Guden et al., 2021). Different bacterial mixtures may produce distinct bacterial quorum sensing signals and/or different types or concentrations of attractants (Köthe et al., 2003; Beale et al., 2006), which may explain the food preferences of *L. marina* (Guden et al., 2021). Nematodes are capable of locating and differentiating the types and abundances of various bacterial strains as food sources (Moens et al., 1999; Newsham et al., 2004; Zhang et al., 2005).

Furthermore, the dispersal behaviour of the three cryptic species of *L. marina* also coincides with their fitness performance. Our prior experiments revealed that a more diverse food source increases nematode fitness of Pm I and Pm IV (Guden et al., 2021, 2024). Thus, Pm I and Pm IV tend to disperse faster toward patches with a more diverse food source, which they prefer and which improves their fitness. This is consistent with previous studies showing that animals tend to feed optimally by choosing food resources that maximize offspring performance (Gripenberg et al., 2010). Our results are striking because the replicates of each food-diversity treatment in our experiment consist of different combinations of bacterial strains, which underlines the importance of food diversity per se on the dispersal of *L. marina*. These findings appear to corroborate the 'balanced-diet hypothesis', which suggests that diverse food sources provide a more complete range of nutritional resources (DeMott, 1998; Pfisterer et al., 2003; Worm et al., 2006). While it would have been more informative if we assessed the nutritional quality of individual bacterial strains used in the experiments, our preliminary analyses revealed that each bacterial strain can support nematode growth. Nevertheless, while Pm III exhibited fast dispersal toward distant patches with medium- and high-diversity food that have also been shown to increase the fitness of this cryptic species (Guden et al., 2021, 2024), patches with *E. coli* also triggered fast dispersal in Pm III regardless of population density (Fig. 3); Supplementary material, Fig. 1). In the lab, all cryptic species of *L. marina* are easily maintained on *E. coli*, and Pm III exhibits the highest fecundity among all the cryptic species with this food source (De Meester et al., 2015b; Guden et al., 2021). The high fitness gain (*e.g.*, high fecundity) of Pm III from feeding on *E. coli* may explain why Pm III exhibits faster dispersal to *E. coli* than the other cryptic species.

The differences in the dispersal behaviour of the cryptic species of *L. marina* depending on food diversity demonstrate that the cryptic species acquire information about their environment when making dispersal decisions, in contrast to the assumptions of previous spatially-explicit ecological models that dispersal is uninformed and random (Patterson et al., 2008). There is now considerable evidence that animals make informed dispersal, *i.e.*, dispersal behavior is not only influenced by the internal state of species (phenotype dependence) but also by external information (condition-dependent) (Clobert et al., 2009), such as a patch's food availability (Aguillon and Duckworth, 2015; Fronhofer et al., 2015; Kreuzinger-Janik et al., 2022). Nevertheless, informed dispersal strategies in cryptic species have rarely been documented (Chenuil et al., 2019).

The influence of food diversity on dispersal may play an important role on the coexistence of cryptic marine nematode species in ecological communities. Marine nematodes are known to be capable of passive and active dispersal. They can passively disperse with the water flow and wind drift, or through rafting on floating items and hitchhiking on larger animals (Thiel and Gutow, 2005; Ptatscheck and Traunspurger, 2020; Buys et al., 2021). Moreover, they can actively disperse by migrating laterally through sediments or by swimming (Ullberg and Ólafsson, 2003; Schratzberger et al., 2004; Thomas and Lana, 2011). In the field, the co-occurring cryptic species of *L. marina* live on both living and decomposing macro-algae in the intertidal zone, and mainly feed on the microbial biofilms attached to the surfaces of macro-algae. These biofilms are highly variable in (micro)space and time: bacterial communities can differ between species of algae and at different temporal scales (Lachnit et al., 2011), and may also vary between two nearby algal patches or between different structures of a single algal plant (De Meester, 2016; Guden et al., 2018). This creates spatial and temporal variability in bacterial assemblage composition, which affect the food resources available for nematodes. The resource landscape for *L. marina* can therefore consist of food resource patches that vary in diversity, and such heterogeneity in food diversity may alter the dispersal behaviour of the cryptic species. The variation in active dispersal of *L. marina* in response to food diversity over small distances as observed in this study may also influence dispersal at larger scales since it can potentially facilitate passive dispersal. In turn, this may have important consequences on species distribution and coexistence of the cryptic species. Our prior experiments revealed that food diversity affects various life-history traits of the cryptic species (Guden et al., 2021) and alters the outcome of intra- and interspecific interactions (Guden et al., 2024, 2021), showing that food diversity enhances niche differentiation between the cryptic species. These effects on niche differentiation, in addition to the impact of food diversity on dispersal behaviour as revealed in the present study, indicate that food diversity may contribute significantly to the coexistence of closely related species.

While the present study has expanded our knowledge on the effects of food diversity on the dispersal of cryptic nematode species, it is important to recognize certain methodological limitations. First, the results are derived from experiments conducted in controlled laboratory conditions using microcosms with a limited number of replicates, and as such may not fully capture the dynamics occurring on a larger scale in the natural environment. Hence, caution is warranted when extrapolating our results to field conditions. Second, due to time constraints since all the experiments had to be started and monitored at the same time, we did not measure mortality rates and nematode density per day, which would have given us more information on the survival and persistence of the nematodes in different food patches. Third, the cryptic species of *L. marina* are exposed to a much higher diversity of resources in nature and more food patches than what was utilized in our study, potentially resulting in different responses. While we cannot fully mimic the diversity of resources in the real world, our research highlights the importance of resource diversity in shaping the behavior and interactions of different cryptic species, and thus may contribute significantly to the coexistence of closely related species in the field.

CONCLUSION

Elucidating the mechanisms that underlie patterns of species distribution and diversity maintenance in ecological communities, is a central objective in ecology. Dispersal is one of the basic life-history strategies of organisms, which can have profound consequences for meta-population dynamics, genetic diversity, and species coexistence. Here, we demonstrate that food diversity alters the dispersal behavior of the different cryptic species of *L. marina*. We reveal that *L. marina* exhibit informed dispersal strategies, indicating that their dispersal behavior is not only influenced by internal attributes, but also by external information. Food diversity can trigger the dispersal of the cryptic species of *L. marina*, exhibiting generally faster dispersal toward patches with more diverse food. The ephemeral nature of food resource patches in the environment where *L. marina* lives may result in changes in the dispersal behavior of the cryptic species, which may facilitate their coexistence in the field.

CONFLICT OF INTEREST STATEMENT

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

DATA AVAILABILITY STATEMENT

All data of the study is publicly available in the Integrated Marine Information System (IMIS) database (VLIZ): https://doi.org/10.14284/610.

AUTHOR CONTRIBUTIONS

RMG was heavily involved in all aspects of the present work, performed all the lab work and data analyses, and wrote the original draft. RMG and TM conceived this study and its sampling design. SD and TM contributed to the writing of the manuscript. All authors contributed to the article and approved the submitted version.

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TABLES

Table 1. Results of the one-way ANOVA tests on the effects of food treatment on the time of nematode dispersal and proportion of nematode dispersers for each cryptic species of *L. marina* in homogeneous and heteregeneous patches. Significant differences ($p < 0.05$) are highlighted in bold.

	Time of Nematode Dispersal		
Species	**df**	**F**	***p*-value**
(A) Effect of food treatment in homogeneous patches			
Pm I	3	291.1	**2.8e-9**
Pm III	3	9.0	**0.004**
(B) Effect of food treatment in heterogeneous patches			
Pm I	3	161.5	**5.8e-10**
Pm III	3	11.8	**0.0007**
Pm IV	3	31.0	**6.3e-06**

	Proportion of Nematode Dispersers		
Species	**df**	**F**	***p*-value**
(A) Effect of food treatment in homogeneous patches			
Pm I	3	39.3	**1.7e-5**
Pm III	3	29.8	**5.3e-05**
(B) Effect of food treatment in heterogeneous patches			
Pm I	3	17.5	**0.0001**
Pm III	3	10.9	**0.001**
Pm IV	3	8.0	**0.003**

Table 2. Pairwise-test results on the differences in the time of nematode dispersal between food treatments for each cryptic species of *L. marina* in homogeneous and heteregeneous patches. Significant differences ($p < 0.05$) are highlighted in bold.

	Time of Nematode Dispersal		
	Pm I	**Pm III**	**Pm IV**
Food treatment	***p*-value**	***p*-value**	***p*-value**
(A) Differences between food treatments in homogeneous patches			
E-E vs L-L	**1.4e-8**	**0.04**	
E-E vs M-M	**1.0e-7**	0.9	
E-E vs H-H	**3.2e-9**	0.2	
L-L vs M-M	**0.02**	0.08	
L-L vs H-H	**0.01**	**0.003**	
M-M vs H-H	**0.0001**	0.2	
(B) Differences between food treatments in heterogeneous patches			
E-E vs E-L	**1.4e-8**	**0.0006**	**0.007**
E-E vs E-M	**7.7e-9**	0.2	**3.2e-5**
E-E vs E-H	**6.0e-10**	0.7	**8.1e-6**
E-L vs E-M	0.8	**0.02**	**0.02**
E-L vs E-H	**0.002**	**0.004**	**0.003**
E-M vs E-H	**0.007**	0.7	0.7

Table 3. Pairwise-test results on the differences in the proportion of nematode dispersers between food treatments for each cryptic species of *L. marina* in homogeneous and heteregeneous patches. Significant differences ($p < 0.05$) are highlighted in bold.

	Proportion of Nematode Dispersers		
	Pm I	**Pm III**	**Pm IV**
Food treatment	***p*-value**	***p*-value**	***p*-value**
(A) Differences between food treatments in homogeneous patches			
E-E vs L-L	0.06	**0.0001**	
E-E vs M-M	**0.0001**	0.9	
E-E vs H-H	**2.1e-5**	**0.02**	
L-L vs M-M	**0.008**	**8.4e-5**	
L-L vs H-H	**0.0007**	**0.01**	
M-M vs H-H	0.3	**0.01**	
(B) Differences between food treatments in heterogeneous patches			
E-E vs E-L	0.08	**0.02**	0.9
E-E vs E-M	**0.02**	0.3	**0.01**
E-E vs E-H	**5.9e-5**	0.7	**0.03**
E-L vs E-M	0.8	**0.001**	**0.02**
E-L vs E-H	**0.003**	**0.003**	**0.04**
E-M vs E-H	**0.01**	0.9	0.9

Table 4. Summary of the results of the dispersal rates and proportion of dispersers for each cryptic species of *L. marina*.

Species	**Dispersal Rate**	**Proportion of Dispersers**
	Homogeneous patches: 'similar patch conditions'	
Pm I	H-H > L-L > M-M > E-E	H-H, M-M > L-L, E-E
Pm III	H-H, E-E, M-M > L-L	L-L > H-H > E-E, M-M
Pm IV	Not tested	Not tested
	Heterogeneous patches: 'different distant-patch conditions'	
Pm I	E-H > E-M > E-L > E-E	E-H > E-M, E-L > E-E
Pm III	E-E, E-H, E-M > E-L	E-M, E-H, E-E > E-L
Pm IV	E-H, E-M > E-L > E-E	E-M, E-H > E-L, E-E

E: *E. coli*; L: low-diversity food; M: medium-diversity food; H: high-diversity food
(>): significantly faster dispersal rate or significantly higher proportion of dispersers
(,): no significant difference between food treatments

FIGURES

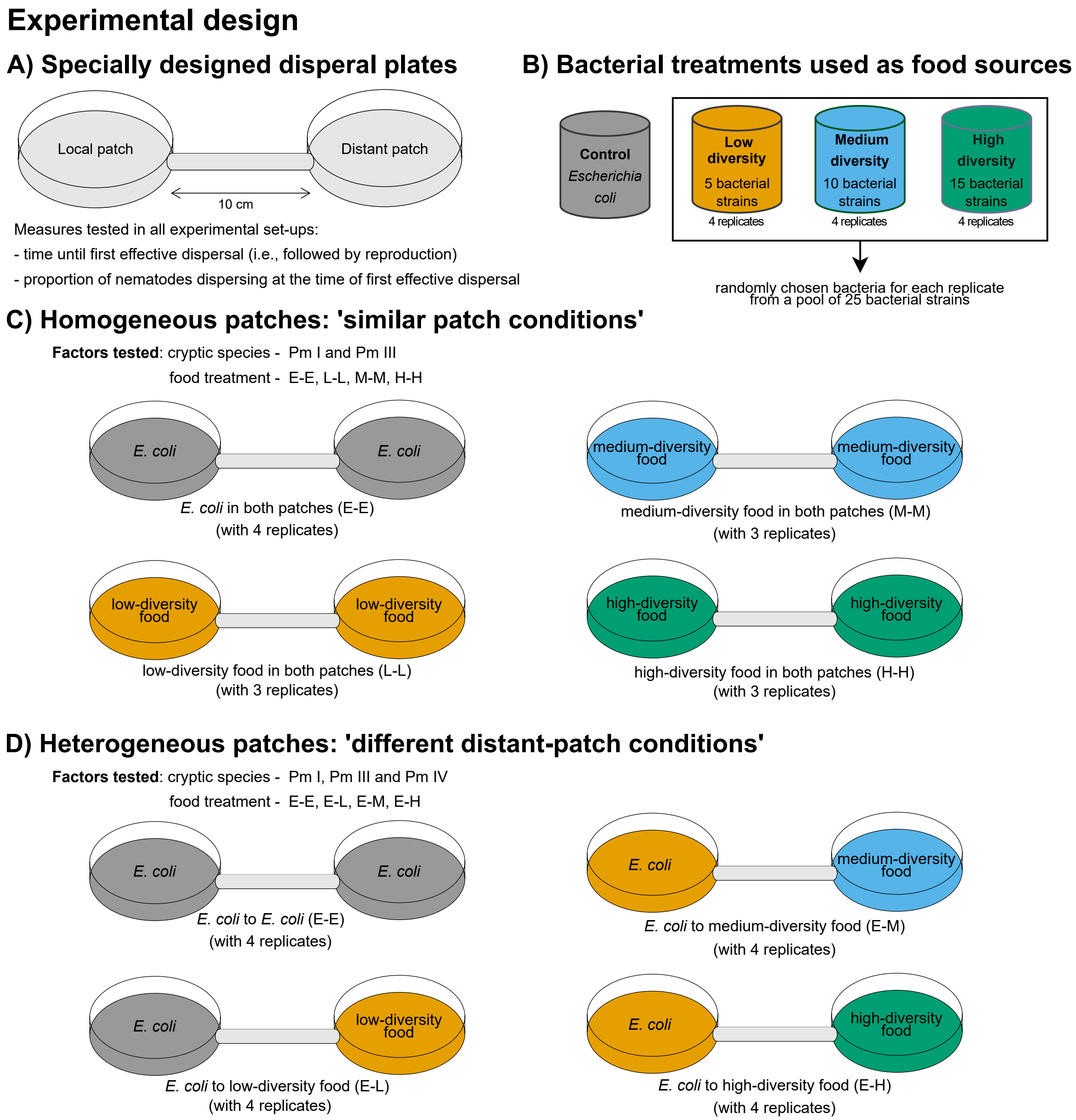

Fig. 1. Summary of the experimental design for testing the effects of food diversity on nematode dispersal. (A) Specially designed dispersal plates and (B) four food-(bacteria) diversity treatments were used in the experiments. The effects of food diversity on the dispersal behavior of *L. marina* were tested in homogeneous and heterogeneous patches. In (C) homogeneous patches, local and distant patches were added with the same food treatments. In (D) heterogeneous patches, local patches were supplemented with *E. coli* and distant patches with different food-diversity treatments to investigate whether food diversity can drive dispersal.

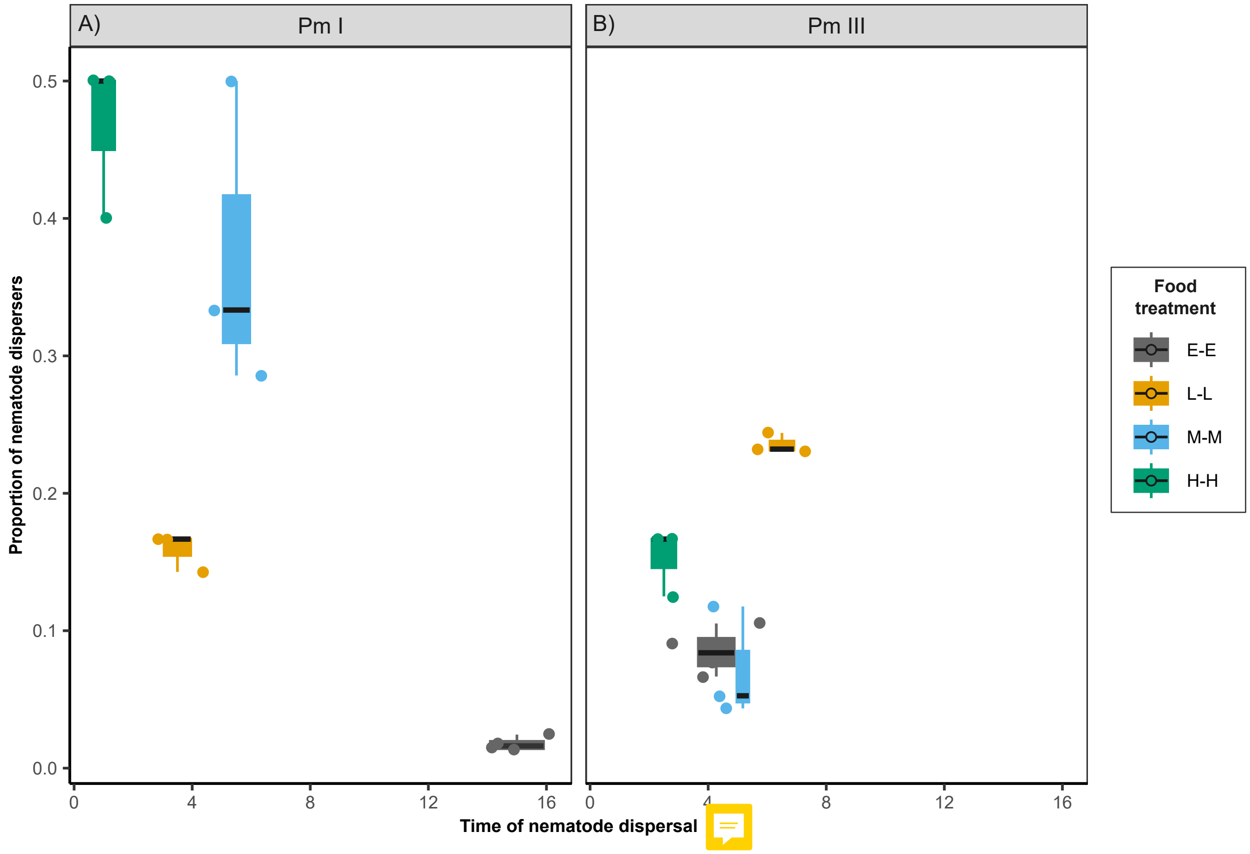

Fig. 2. Effects of food diversity on nematode dispersal for the cryptic species of *L. marina* in the setup consisting of homogeneous patches with the same food treatments in local and distant patches. The boxplot shows the time of nematode dispersal and proportion of nematode dispersers (mean ± SE) in homogeneous patches for (A) Pm I and (B) Pm III. Food treatments in both patches consist of *E. coli* (E-E), low-diversity food (L-L), medium-diversity food or high-diversity food (H-H) (*n* = 4).

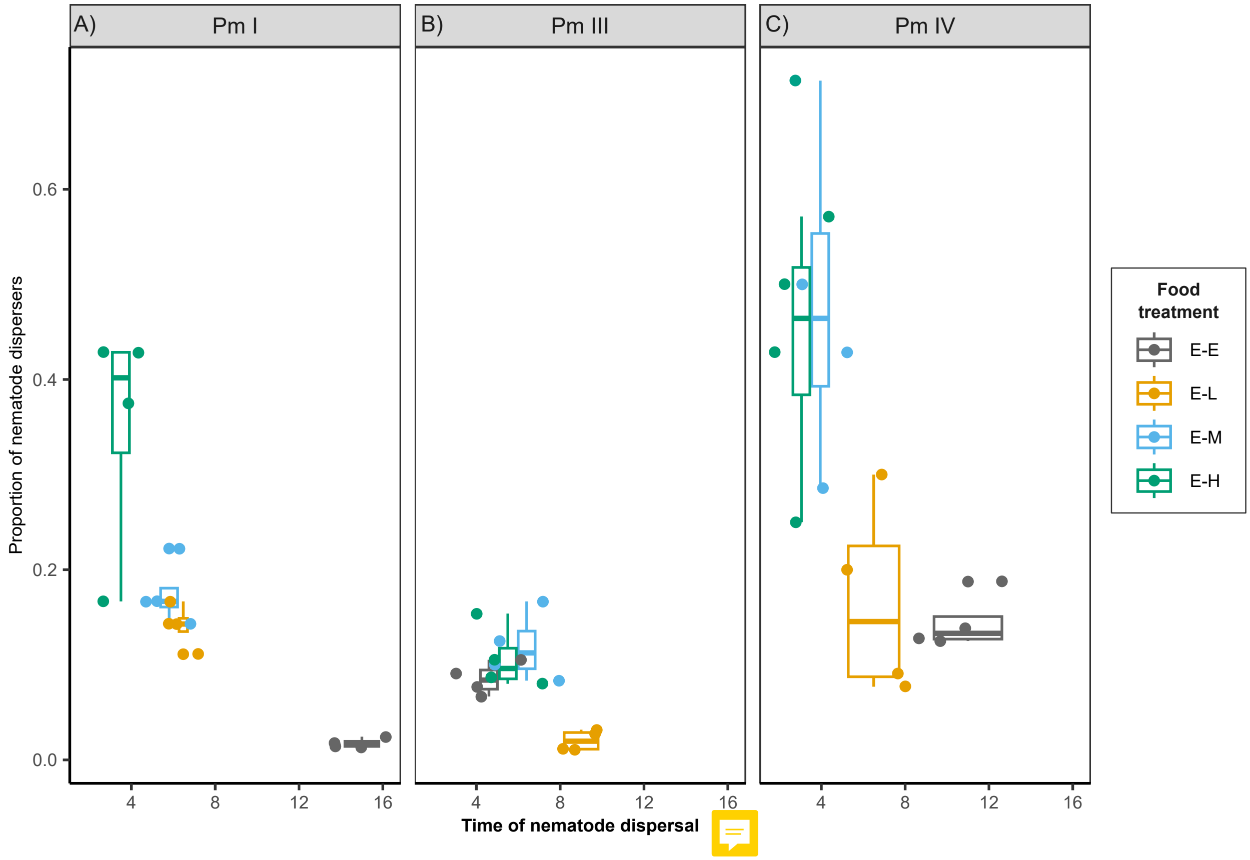

Fig. 3. Effects of food diversity on nematode dispersal for the cryptic species of *L. marina* in the setup consisting of heterogeneous patches with *E. coli* in the local patches and different food treatments in the distant patches. The boxplot shows the time of nematode dispersal and proportion of nematode dispersers (mean ± SE) in homogeneous patches for (A) Pm I, (B) Pm III, and (C) Pm IV. Food treatments consist of a single strain resource *E. coli* in local patches and *E. coli* (E-E), low-diversity food (E-L), medium-diversity food (E-M), or high-diversity food (E-H) in the distant patches (*n* = 4).

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