Genetic signature of the colonisation dynamics along a coastal expansion front in the damselfly *Coenagrion scitulum*

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Abstract. 1. Many insects are expanding their distribution range polewards as a result of climate change, which has been shown to be associated with founder effects leading to a reduction in genetic diversity and an increase in genetic differentiation. These spatial genetic patterns may arise from colonisation from a broad expansion front or a limited neighbourhood after a stepping stone model of dispersal. The temporal persistence of such founder effects are poorly understood, mainly because studies looking at the fine-scale initial temporal dynamics of the genetic signature of a range expansion are rare.

2. Using microsatellite markers, we performed a detailed spatiotemporal genetic analysis of the range expanding damselfly *Coenagrion scitulum* (Rambur) along a coastal axis during the first years after colonisation.

3. A decrease was in (private) allelic richness when going northwards along the coastline, which is consistent with a scenario of cumulative founder events. In spite of the spatiotemporal dynamics in the observation records of the species along the coastline, the spatial genetic data indicated a major contribution from the broad expansion front during the colonisation of the coastline rather than a stepping-stone colonisation process.

4. The fine-scale temporal dynamics of the range expansion indicated the absence of persistent founder effects and instead showed considerable temporal instability in genetic indices at the more northern edge populations. This may be explained by genetic immigration and admixture from the broad expansion front in this active disperser.

Key words. *Coenagrion scitulum*, founder effect, genetic diversity, isolation-by–colonisation, range expansion.

Introduction

Many species are moving poleward in response to climate change (Hickling *et al.,* 2006). In spite of the numerous examples of range expansions driven by climate change (Davis & Shaw, 2001), empirical studies on the genetic effects of the recent range expansions remain scarce (McInerny *et al.,* 2009). Nevertheless, evolutionary processes can feedback on the rate of

range expansion and the ability to adapt to a changing environment (Phillips, 2012). As it is expected that global warming will continue to affect species' ranges, it is important to investigate evolutionary processes during range expansion and in a broader perspective how species are and will be coping with global warming. Range expansion occurs through colonists that originate from a broad expansion front or a limited neighbourhood after a stepping stone model of dispersal (Le Corre & Kremer, 1998). Both mechanisms of range expansion may result in founder effects, whereby genetic variation at the range front is

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lost thereby causing spatial patterns in genetic differentiation and variation. However, the two modes of expansion can lead to different patterns in genetic diversity and differentiation. While during a stepping stone expansion genetic drift will be a driving force, a broad expansion front will be more characterised by gene flow. The effect of serial founder events in a stepping stone model leads to a gradual decrease in genetic diversity and an increase in genetic differentiation going further from the source (Hallatschek *et al.*, 2007; Excoffier *et al.*, 2009), especially when newly established populations originate from a low number of founders (Nei *et al.*, 1975; Le Corre & Kremer, 1998). The few existing studies have shown that serial founder events indeed may cause an immediate reduction in genetic diversity during rapid range expansion (Watts *et al.*, 2010; Garroway *et al.*, 2011). Genetic effects are, however, expected to be less profound when edge populations are established from a broad expansion front where multiple founder events from different source populations are more likely, and gene flow among populations is more important (Excoffier *et al.*, 2009).

While most attention went to the spatial genetic signature of range expansions, much less attention went to the fine-scale temporal dynamics in the genetic signature of the associated founder events. In general, the degree to which founder effects persist and remain detectable over time largely depends on the extent of realised gene flow after founding (De Meester *et al.*, 2002). When founder effects persist over time and reflect the colonisation history, they form a pattern of isolation-by-colonisation (IBC), with pairwise genetic differentiation and the scatter in pairwise genetic differentiation increasing with distance identical to a pattern of isolation by dispersal limitation (Hutchison & Templeton, 1999; Orsini *et al.*, 2013). Patterns of IBC persisting over decades to millennia have been observed in many organisms, from humans to zooplankton, and across spatial scales spanning only a few tens of kilometres to a global scale (Pruett & Winker, 2005; Ramachandran *et al.*, 2005; Gouws & Stewart, 2007; Chatzimanolis & Caterino, 2008; Ventura *et al.*, 2014). Although founder effects are most likely to persist in the face of dispersal limitation, they can sometimes persist even in the presence of high dispersal (e.g. Ventura *et al.*, 2014) as is typically the case during rapid range expansions (Travis *et al.*, 2013). The persistence through time of founder effects under high dispersal is expected when there is rapid local adaptation of the first founders, thereby reducing realised gene flow of later, non-adapted immigrant genotypes (monopolisation scenario, De Meester *et al.*, 2002; reviewed in Orsini *et al.*, 2013). Such rapid local adaptation has indeed been observed in edge populations at moving range fronts (Hill *et al.*, 2011; Therry *et al.* 2014a,2014b) making persistent patterns of IBC during range expansions likely.

We here study the spatial and fine-scale temporal dynamics of the natural range expansion by the Mediterranean damselfly *Coenagrion scitulum* (Rambur). This species has established populations more than 100 km northeastward from its historical range in 10 years time along a broad expansion front in Belgium, Germany, the Netherlands, and Great Britain (see references within Swaegers *et al.*, 2013; Fig. 1a,b). At this large geographical scale, Swaegers *et al.* (2013) showed an increase in genetic differentiation at the edge populations and a subtle decrease in allelic richness, reflecting mild founder effects. We here extend previous study by focusing on the genetic processes on a more local scale, along the North Sea coastline, and by incorporating fine-scale temporal dynamics allowing testing hypotheses about changes in the degree of drift and migration after the establishment of new populations. First, we will test whether at this local scale the genetic signature reflects a stepping stone colonisation process and the associated serial found effects (creating a pattern of IBC) or rather colonisation from the broad expansion front. Although the species shows a broad expansion front at its northern range edge (Swaegers *et al.*, 2013), the first sites colonised in Belgium and the Netherlands were located along a narrow strip of the North Sea coastline. These coastal ponds have been gradually colonised from 2003 onwards with recordings in 2012 at sites 90 km further along the coastline (Fig. 1c). These recordings suggest a range expansion in a linear stepping-stone fashion, which is expected to be accompanied by cumulative founder events giving rise to losses in genetic diversity and the augmentation of genetic differentiation if the number of founders is low (Hallatschek *et al.*, 2007; Excoffier *et al.*, 2009). Second, we will test for fine-scale temporal patterns in the genetic signature of the range expansion. Given that range expansion is associated with (the evolution of) high dispersal (Travis *et al.*, 2013, for the study species: Therry *et al.*, 2014a,2014c), we may expect that founder events will be less profound (Excoffier *et al.*, 2009). Yet, as common garden experiments have also shown rapid evolution with regard to life history (e.g. elevated growth rate) in the edge populations at the moving range front of this species (Therry *et al.*, 2014a,2014b) and adaptations to a shorter larval growth season (Therry *et al.*, 2014d), we may as well expect founder effects to linger at least during the first years after colonisation (De Meester *et al.*, 2002; Orsini *et al.*, 2013). To address these questions, we therefore sampled the coastline over the initial years of colonisation and also included populations from the broader range front. Specifically, this allows testing whether genetic signals of founder effects persist during the first years after colonisation of new areas of a natural range front forming a pattern of isolation by colonisation or are overridden by recurrent genetic input from the broad expansion front.

Materials and methods

The damselfly *C. scitulum* has a primarily Mediterranean distribution (Dommanget *et al.*, 1994; Dijkstra, 2006; Jean-Pierre Boudot, unpublished; Fig. 1a). In the early 1990s the northern edge of the range was situated in Northern France. The species has recently expanded its range and founded edge populations in an eastward, northward, and westward direction (references within Swaegers *et al.*, 2013, the colonisation of Belgium is visualised in Figure S1). Samples for this study were collected from ponds along the coastline from northern France, Belgium, and southern Holland during the single flight period of the species in June–July from 2010 to 2012 (Fig. 1b, Table 1). Damselflies have a complex life cycle with an aquatic larval stage and an adult terrestrial stage where dispersal occurs (Stoks & Cordoba-Aguilar, 2012). Given that *C. scitulum* breeding ponds in the current study were separated >1 km from each other and
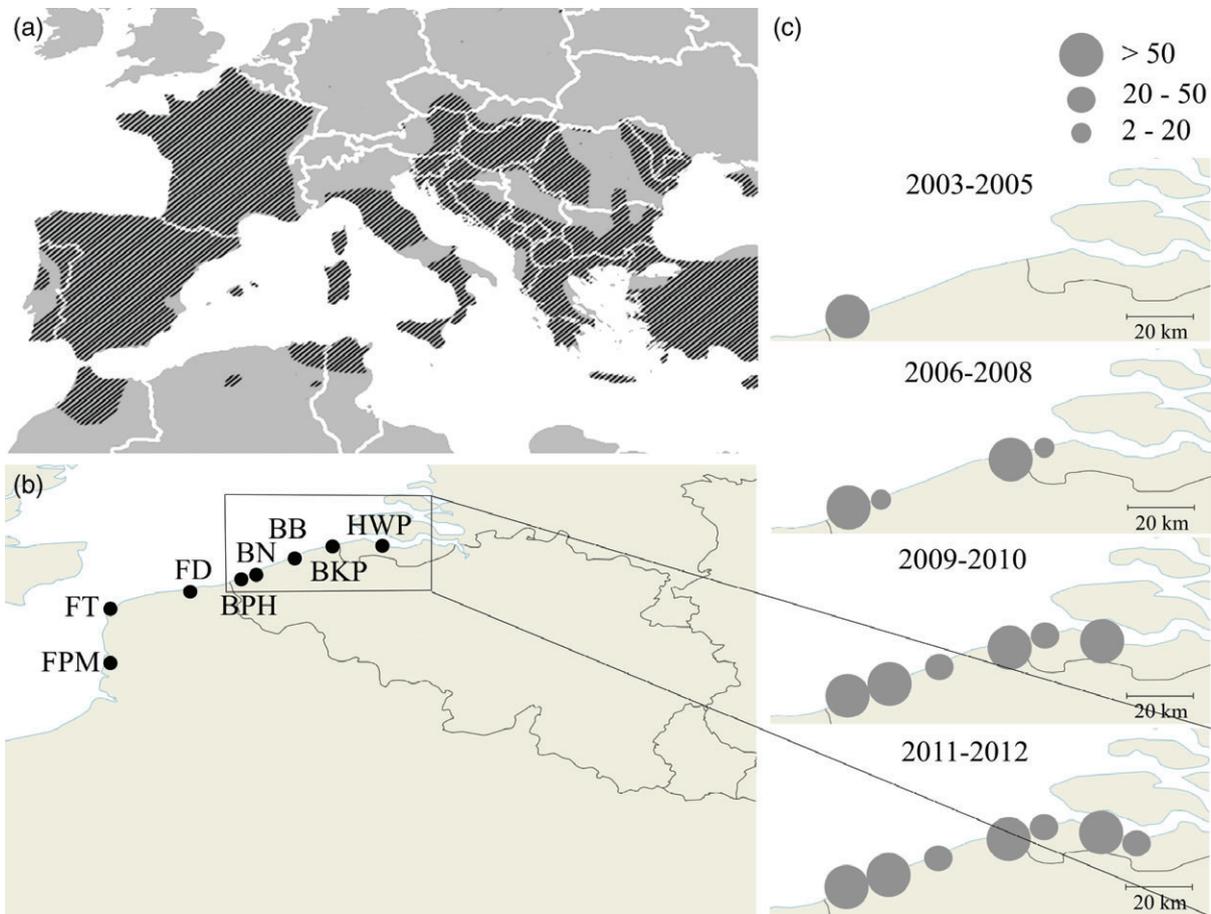
Fig. 1. (a) Map of the historical (before 1990) core distribution of *Coenagrion scitulum* based on Dommanget *et al.*, 1994; Dijkstra (2006); Jean-Pierre Boudot, unpublished, (b) map of the sampled localities in Belgium, Holland, and Northern France, (c) schematic overview of the range expansion history along the Belgian and Dutch coast (based on waarnemingen.be and waarnemingen.nl). The size of the circles represents the maximum number of individuals that has been recorded that period.

C. scitulum adults show very low exchange between nearby (200 m) ponds during the breeding season (Angelibert & Giani, 2003), each study pond probably represents a separate population. Note this does not have to contradict the rapid range expansion of the species as this may be driven to a large extent by the animals in the tail of the dispersal kernel. Two ponds were sampled twice and two other ponds were sampled in three consecutive years. In addition, two inland ponds were sampled to infer the possible influx from the broad expansion front. As *C. scitulum* is univoltine in its core area (Cayrou & Céréghino, 2005) and breeding experiments in addition to observations in the field indicate that voltinism has not changed during range expansion (Therry *et al.*, 2014a) samples at the same pond in different years represent different generations.

We genotyped 114 damselflies at 11 microsatellite markers as described in Johansson *et al.* (2011) and Swaegers *et al.* (2012). In a preliminary step, all populations were tested for the Hardy–Weinberg equilibrium and deviations from linkage equilibrium using GENEPOP (Rousset, 2008). After Bonferroni's correction, one population (NWP) showed a deviation from the Hardy–Weinberg equilibrium at locus cosci_05 (see File S1).

No significant linkage disequilibrium was detected. These samples were combined with 151 individuals that had been genotyped at the same loci for a phylogeographic study (Swaegers *et al.,* 2014). This resulted in 265 samples from eight populations across the studied coastline (Fig. 1b). In addition, 24 samples were genotyped from the two inland populations in Belgium (BKW and BRP, Fig. 1b). We calculated expected heterozygosity (H_e) using Genalex (Peakall & Smouse, 2006) and allelic richness (AR) and private allelic richness (PAR) using a rarefaction approach in the software ADZE (Szpiech *et al.,* 2008) both with a minimum number of individuals equal to 11. Nei's (1972) pairwise standard genetic distance was calculated to estimate genetic differentiation between every population pair. In contrast with other measures of differentiation (such as F_{ST}), Nei's distance changes monotonically with allelic differentiation (Jost, 2008).

To test the effect of the northward colonisation on the genetic diversity and structure, we used linear mixed models (GLMM) with either allelic richness, heterozygosity, private allelic richness as dependent variables and the year of sampling as well as the distance to the French coastal core population FPM

Table 1. Overview of the sampled coastal sites (displayed on Fig. 1c), the sampling year, sample size (*n*), the distance from the most southern sampled population (FPM), expected heterozygosity (H_e), allelic richness (AR), and private allelic richness (PAR).

Site	Sampling year	n	Distance to FPM (km)	H_e	AR	PAR
FPM	2010	15	0	0.622	5.88	0.212
FPM	2011	15	0	0.628	6.2	0.555
FPM	2012	14	0	0.651	6.01	0.348
FT	2011	11	48.38	0.614	6.12	0.603
FD	2011	12	94.36	0.614	5.71	0.142
BPH	2010	12	121.58	0.632	5.76	0.22
BPH	2011	11	121.58	0.622	5.39	0.115
BN	2010	14	130.74	0.622	6.19	0.184
BB	2011	11	153.23	0.567	5.12	0.14
BKP	2010	13	180.31	0.644	5.26	0.092
BKP	2011	17	180.31	0.633	5.65	0.106
NWP	2010	31	199.35	0.668	5.77	0.146
NWP	2011	13	199.35	0.673	5.29	0.099
NWP	2012	15	199.35	0.649	5.11	0.181

(calculated as the linear distance along the shore) or latitude as predictor variables. Note that we used distance to FPM as a predictor to a explicit test for a stepping-stone colonisation process along the coast, thereby assuming FPM being the source population. In addition, we also used latitude as a predictor to test for an effect of the broad range front. We also explicitly tested for a correlation between distance to FPM and latitude as, in that case, both mechanisms may be apparently supported and more detailed genetic analyses (see below) are needed to disentangle these alternatives. Population was considered a random factor. We validated the GLM assumptions of normality and homoscedasticity of the residuals by visual inspection of residual plots in R (R Core Team, 2014).

To obtain normally distributed residuals we log-transformed private allelic richness. For pairwise genetic distance values, the same model was fitted using distance-based redundancy analysis (Legendre & Anderson, 1999) in which Nei's (1972) genetic distance values were used as the response dissimilarity matrix. This analysis was performed with *capscale* within the vegan package 2.0-2 (Dixon, 2003). The significance of the constraints (distance to FPM and year) was tested using a permutation test (1000 permutations) with populations sampled more than once being grouped during the randomisation. We also calculated pairwise F_{ST}s (Weir & Cockerham, 1984) to allow comparison with other studies.

To test in more detail for signals of a stepping-stone colonisation process and colonisation from the broad range front, we analysed the genetic structure using STRUCTURE (Pritchard *et al.,* 2000). This analysis assigns individuals to clusters based on their multilocus genotypes. Correlated allele frequencies were assumed, and the admixture model simulations were run with prior information on the site and year of sampling. Runs were performed using a burn-in period of 20 000 replicates and a sampling period of 100 000 replicates. Simulations were run for a number of clusters (K) ranging from 1 to 10, and 20 iterations were performed for each K. The log likelihoods from

these iterations were averaged for each K and the most likely K was selected with the delta K method (Evanno *et al.,* 2005) using STRUCTUREHARVESTER (Earl & von Holdt, 2011). The software CLUMPP was used to align the replicate runs with the option 'greedy' (Jakobsson & Rosenberg, 2007). The detection of one cluster might suggest gene flow between populations is high enough to conserve genetic uniformity. If, on the other hand, geographic clusters are found, populations might either have experienced genetic drift leading to genetic differentiation or genetic input from different sources.

Results

The sampled populations of *C. scitulum* showed a significant decrease in allelic richness and private allelic richness with increasing distance from the putative source region (NW-France, FPM) ($P < 0.05$, Fig. 2, Table 2, AR: $R^2_{adjusted} = 0.438$, PAR: $R^2_{adjusted} = 0.648$), which is consistent with the recorded colonisation of formerly vacant habitat in Northern areas. For private allelic richness, this pattern varied between years. The decrease in the private allelic richness was more significant in 2011 (Table S1a). By contrast, there were no expected effects of distance from FPM on heterozygosity and pairwise genetic distances. Heterozygosity increased further away from FPM, yet only significantly in 2010 ($P < 0.05$, Table S1, $R^2_{adjusted} = 0.140$). There were no significant effects of the distance from FPM or sampling year on pairwise genetic distances (Table 2a). The distance to FPM and latitude were highly correlated ($r = 0.98$, $P < 0.05$) leading to similar patterns in the measured genetic indices. Indeed, when latitude instead of the distance to population FPM was included in the model, allelic richness also significantly decreased when going northwards ($P < 0.05$, $R^2_{adjusted} = 0.398$, Table 2b, Table S1). Also for private allelic richness (decreasing) and heterozygosity (increasing), the same patterns with latitude were detected as in the analysis where distance to FMP was fitted (PA: $R^2_{adjusted} = 0.564$,He: $R^2_{adjusted} = 0.680$, Table 2b, Table S1). Also analogously with the distance to FPM, no effect of latitude on the pairwise genetic distances was found (Table 2b). Genetic differentiation measured by pairwise F_{ST}s among sample pairs was generally low, varying from 0 up to 0.1 (Table S2).

Three genetic clusters were detected in the STRUCTURE analysis (Fig. 3) showing considerable genetic structure on this relatively small scale. Several patterns can be visually derived from this analysis. Individuals from the most southern French coastal core population FPM were almost completely assigned to a first cluster (dark grey, Fig. 4). Individuals of the southern and central Belgian coastal populations BN, BPH and BB were also assigned to this cluster with a high probability relative to the remaining populations. For the more northern Belgian population BKP this probability increased in 2011. Yet, individuals of the other two French coastal populations northwards from FPM (FT and FD) were also partly assigned to a second cluster (black, Fig. 4). The populations BPH, BKP and NWP that were sampled in 2010 were also partly assigned to this cluster. Finally, the most recently founded northern populations in Belgium (BKP) and Holland (NWP) were also partly assigned to a third cluster
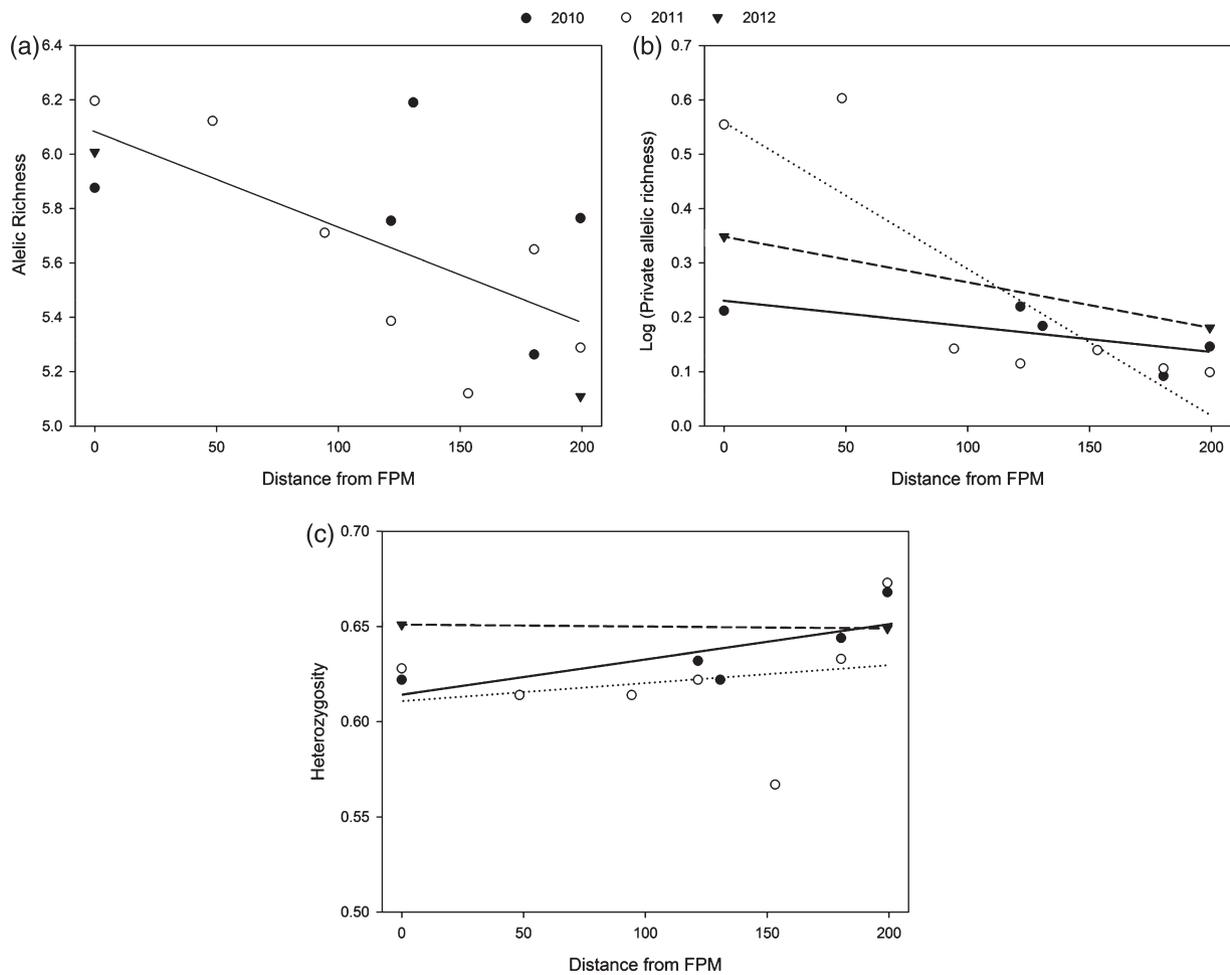
Fig. 2. Geographical patterns of genetic diversity across the coastal populations as a function of the distance to the putative source region (NW-France, core population FPM): (a) allelic richness, (b) private allelic richness, and (c) heterozygosity. When the interaction between sampling year and distance to FPM was significant, all three slopes were plotted. Regression lines are obtained from the generalised linear model (GLM) analyses reported in Table 2.

(light grey, Fig 4). For NWP, the probability that an individual was assigned to the third cluster increased in 2011 and 2012. Furthermore, in 2010 the coastal populations BKP and NWP shared the same genetic composition as the inland population BKW that was also included in the analysis. Both inland populations were mainly assigned to the second cluster (dark grey, Fig. 4).

Discussion

In this study, we performed a detailed spatiotemporal genetic analysis of the range expanding damselfly *C. scitulum* along a coastal axis during the first years after colonisation. The two novel key findings of the current study that extend previous insights obtained in the large-scale study of this range expansion (Swaegers *et al.*, 2013, 2014) are that (i) the spatial dynamics indicate founder effects and a major contribution from the broad expansion front during the colonisation of the coastline rather than a stepping-stone colonisation process and (ii) the fine-scale temporal dynamics do not reflect persistent founder effects

and instead show considerable temporal instability in genetic indices.

In spite of the spatiotemporal pattern in the observation records suggesting a stepping-stone colonisation along the coastline, the combined spatial genetic evidence indicated a major contribution from the broad expansion front during the colonisation of the coastline. The decrease in (private) allelic richness when going northwards along the coastline is consistent with a scenario of cumulative founder events along the sampled populations. The finding that the signal is not present in the heterozygosity estimates is expected as allelic richness and the private number of alleles are more sensitive to founder effects than heterozygosity (Nei *et al.*, 1975). This result is similar to the findings of Watts *et al.* (2010) and Garroway *et al.* (2011) who also reported a significant decrease in allelic richness in recently established edge populations of the damselfly *Erythromma viridulum* (Charpentier) and in flying squirrels [*Glaucomys volans* (Linnaeus)], respectively. Although the gradually established populations along the sampled coastline

Table 2. Results of the general linear model analysis and of the distance-based redundancy analysis of the effects of the distance to the population FPM (distFPM, a) or latitude (b) the sampling year and their interaction on the three studied genetic diversity indices (He: expected heterozygosity; AR: allelic richness; PAR: private allelic richness) or pair-wise genetic distance values. When the interaction term had a *P*-value larger than 0.10 it was excluded from the full model (non-significant interaction terms not given).

| | General linear model | | | | | | | | | Distance-based RDA | | |
| | H_e | | | AR | | | PAR | | | Genetic distance | | |
	d.f.	*F*	*P*	d.f.	*F*	*P*	d.f.	*F*	*P*	d.f.	*F*	*P*
(a)												
Year	2;14	12.51	**0.0074**	2;14	1.36	0.2878	2;14	3.80	0.0481	2;14	0.5136	0.563
distFPM	1;14	0.06	0.8192	1;14	17.19	**<0.001**	1;14	28.83	**<0.001**	1;14	0.6128	0.606
Year × distFPM	2;14	20.65	**0.0021**	–	–	–	2;14	5.55	**0.0168**	–	–	–
Adjusted R^2 of model	0.140	–	–	0.438	–	–	0.648	–	–	–	–	–
(b)												
Year	2;14	23.58	**0.0015**	1;14	1.39	0.2809	2;14	4.37	**0.0334**	2;14	1.0627	0.358
Latitude	1;14	0	0.9479	2;14	14.95	**0.0017**	1;14	22.52	**0.0003**	1;14	0.8159	0.561
Year × latitude	2;14	23.55	**0.0015**	–	–	–	2;14	4.37	**0.0335**	–	–	–
Adjusted R^2 of model	0.680	–	–	0.398	–	–	0.564	–	–	–	–	–

Significant *P*-values (<0.05) are shown in bold.
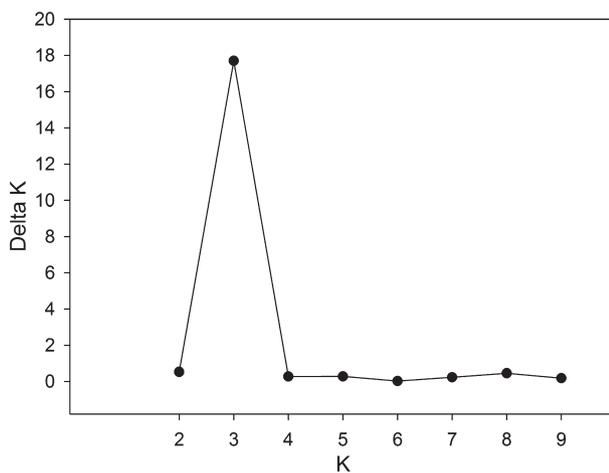
Fig. 3. Support (delta K value) for scenarios with a different number of genetic clusters based on a STRUCTURE analysis.

genetically thus reflect stepping-stone colonisation, the same patterns were upheld using latitude as a predictor as these two variables were highly correlated. This indicated that the genetic signal of stepping-stone expansion might as well be a signal of expansion of a broad front. More conclusive evidence for a major contribution from the broad expansion front during the colonisation of the coastline came from the genetic assignment analysis. This analysis showed that the adjacent populations are only weakly genetically similar to FPM and that individuals of the edge populations (BKP, NWP) have fundamentally different genetic characteristics from FPM and other more Southern coastal populations while they shared a similar genetic composition as the nearby inland population BKW. This might also have contributed to the higher expected heterozygosity in these two edge populations. Also, the expected increase in genetic differentiation under a stepping-stone model (isolation by colonisation) at the expanding range front could not be detected. The

level of pairwise genetic differentiation calculated using F_{ST} was overall low (range 0–0.1) and similar to other odonate studies where values ranged from 0 to 0.157 (Watts *et al.*, 2006, 2010; Johansson *et al.*, 2012).

With regard to the fine-scale temporal dynamics, the data did not indicate persistence of founder effects and showed an unstable genetic pattern at the most recently established edge populations. The genetic assignment results as well as the significant interactions between the sample year and the distance from the putative source region (NW-France, FPM) or latitude for private alleles and heterozygosity, point to a clear temporal instability in genetic structure. This is in contrast to a study on the genetic structure of another expanding damselfly where no strong temporal component to genetic variation was found suggesting a persistent founder effect (Watts *et al.*, 2010).

Populations at an expansion front can be expected to be in a non-equilibrium condition, showing fine-scale temporal dynamics (Boileau *et al.,* 1992). This can either be as a result of strong genetic drift and large year-to-year fluctuations in population size caused by suboptimal habitats (Eckert *et al.,* 2008) or because of migration with a continuous influx of new migrants from the source populations (Excoffier *et al.,* 2009). As our sampling period only encompasses 3 years, and as effective population sizes between edge and core populations differ on average by less than a factor 2 (Swaegers *et al.,* 2013) it seems unlikely that drift alone accounts for the change in genetic structure over time in edge populations. A complete recolonisation of the ponds or sampling of transient migrants at BKP and NWP in 2011 is also unlikely as population densities have been recorded to be high throughout all 3 years (L. Therry, pers. comm). Instead, our results suggest besides drift a major role of migration and admixture from a broad expansion front. Migration is expected to account for a large part of the genetic variability between years as a persistent founder effect is not expected to radically change the genetic structure over time (Orsini *et al.,* 2013). This combination of genetic drift and migration has also been shown to drive the genetic structure in
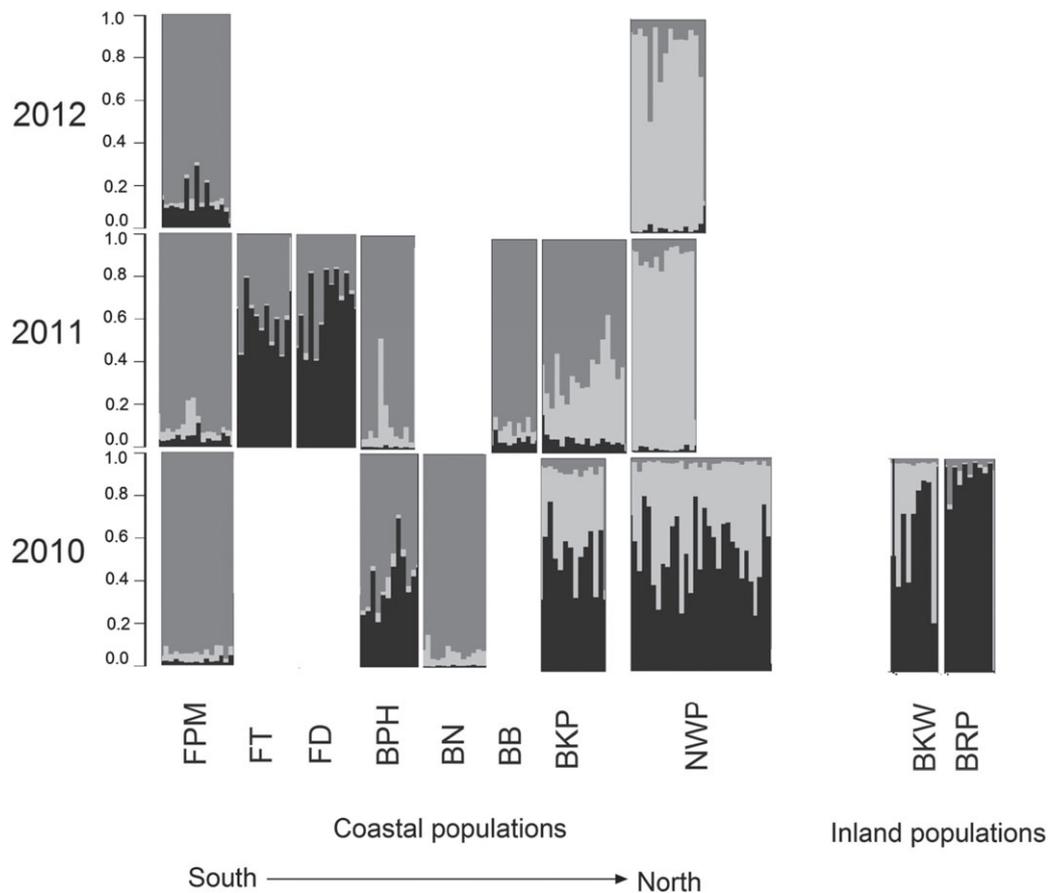
Fig. 4. Visual representation of genetic assignment results showing three genetic clusters, presented per sampling year. The three detected clusters are represented by different colours. Within each individual, the proportion of each colour indicates probability of membership to the given cluster. Populations are separated by white vertical lines and ordered from south (left) to north (right).

recently established populations of the damselfly *E. viridulum* (Watts *et al.*, 2010) and several invasive species (e.g. Herborg *et al.*, 2007; Short & Kenneth Petren, 2011). Although the spatial scale involved here is small (200 km), persistent founder effects have been observed at similar scales in other invertebrate taxa with both high and low dispersal capacity (Gouws & Stewart, 2007; Ventura *et al.,* 2014). Our results, however, show that the predicted reduction in genetic diversity does not necessarily persist as a result of genetic immigration and admixture from a broad expansion front. This also indicates that any adaption at the range front (Therry *et al.* 2014a,2014b) did not strongly buffer against immigrants.

The amount of available genetic diversity has been shown to influence the colonisation success of a species (Hufbauer *et al.,* 2013), and can decrease resistance to stress such as diseases (Spielman *et al.*, 2004). Therefore, it is important to understand the degree in which natural range expansion can influence genetic diversity so that conservation managers are aware of its implications and are able to identify the areas of highest evolutionary potential. Our study thereby cautions against the use of spatiotemporal patterns in observer records when identifying putative sources of colonisation, and illustrates

the need for detailed spatial and fine-scaled temporal genetic analyses to unravel patterns of colonisation.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference:
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Figure S1. Overview of the colonisation of Belgium from 1998 to 2012. Recordings were obtained from the Database Flemish Dragonfly Society, the common database of the ngo Natuurpunt Studie, and the Flemish Dragonfly Society via the online application waarnemingen.be, and from the database of the Walloon Dragonfly Working. For the Flemish data, only recordings of more than one individual were plotted.

Table S1. Description of fixed effects for the mixed general models of expected heterozygosity (He), allelic richness (AR), and log-transformed private allelic richness (PAR). (a) Model with distance from FPM as a predictor. (b) Model with latitude as a predictor.

Table S2. Lower triangle: pairwise F_{ST}s for the coastal populations.

File S1. Genotyping.

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