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# OIKOS

## Research article

# On the role of niche specialization in the geographic distribution of aphid asexual lineages: a case study using the leaf-curl plum aphid superclones

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Asexual lineages often exhibit broad distributions and can thrive in extreme habitats compared to their sexual counterparts. Several hypotheses can be proposed to explain this pattern. Asexual lineages could be versatile genotypes with wide environmental tolerance, enabling their dispersal and persistence across large geographic areas. Alternatively, asexual genotypes could be ecological specialists that thrive in specific environments and outcompete relative colonizing distantly related with similar conditions in the process. Several aphid species feature widespread obligate asexual lineages, commonly known as ‘superclones’. Yet it is often unknown whether these clones are widespread ecological generalists or successful specialists. To explore these hypotheses, we examined climatic niche differentiation among six globally distributed obligate asexual lineages of the cosmopolitan aphid pest, *Brachycaudus helichrysi*. To ensure that we were investigating the aphid genotype niche and not a by-product of their association with endosymbionts mediating thermal tolerance, we first verified that clones hosted similar endosymbiont communities. Subsequently, we conducted multivariate analyses on clone occurrence data on a worldwide scale. Our results revealed that, despite their global distribution, *B. helichrysi* superclones occupy different climatic niches. This study represents the first evidence that aphid superclone distribution can be mediated by distinctive ranges of climatic tolerance.

Keywords: *Brachycaudus helichrysi*, clonality, endosymbionts, frozen niche variation, general-purpose genotype, parthenogenesis

## Introduction

Understanding the ecological differentiation processes underlying the transition from sexuality to asexuality has been a longstanding conundrum for evolutionary biologists (Schön et al. 2009). Given the fast reproductive rates of asexual lines, they can rapidly



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spread and outcompete their sexual relatives when they meet the right conditions. A common pattern to many biological systems encompassing sexual and asexual reproduction is the occurrence of persistent asexual lineages with wide geographic distributions, some of them being also able to occupy disturbed habitats and, more generally, environments with extreme conditions (this pattern is known as 'geographical parthenogenesis') (Vandel 1928, 1940). Several hypotheses can be proposed to explain the emergence, spread, and long-term persistence of these successful asexual lineages. They could owe their persistence and spread across extensive geographical areas to a great phenotypic plasticity. They would represent some sort of ecological generalist whose fast propagation has been facilitated by clonal reproduction. This partly meets the general-purpose genotype (GPG) hypothesis, originally proposed to explain the ubiquity of weedy plants (Baker 1965), which predicts the emergence of asexual lineages with broad environmental tolerances (Parker et al. 1977, Lynch 1984). Alternatively, the maintenance of clonal lineages could be associated with ecological specialisation. Clonal genotypes that are highly successful in specific environmental conditions could efficiently use underutilised resources and outcompete their sexual relatives or other asexual lines (Vrijenhoek 1979, 1984, Pluess and Stöcklin 2005, Vrijenhoek and Parker 2009). This shares similarities with the hypothesis known as the 'frozen niche variation' (FNV) hypothesis (Bell 1982), which proposes that repeated transitions to asexuality result in the selection of locally adapted genotypes from sexually reproducing populations (Vrijenhoek 1979, 1984, Vrijenhoek and Parker 2009).

The specialist versus generalist hypotheses have been explored in a wide range of asexual organisms (reviewed by Vrijenhoek and Parker 2009, and by Fazlioglu and Bonser 2016 for a meta-analysis on plants). Several approaches have been employed in the study of asexual lineages niche breadth: 1) experimental approaches that compare the fitness of asexual clones along environmental gradients under controlled conditions; and 2) empirical approaches that analyse the distribution and realised ecological niches of different asexual clones (Vrijenhoek and Parker 2009). While comparing the response of different asexual lineages to different environmental factors seems to be the most direct method for testing whether they are generalist genotypes or rather efficient specialists, this approach remains challenging as it requires being able to breed different asexual lineages of the same species under laboratory conditions, which is not feasible for all organisms. Empirical studies that look at associations between genetic lineage and environmental variables overcome these difficulties; however, they often come with their own set of limitations. For instance, in early studies that use distributional data, clonal lineages of the same species were sometimes considered as a single unit. Their ecological niche was then compared to that of their sexual relatives to explore whether they have narrower or broader niches, without distinguishing whether clonal populations were composed of multiple independent clonal lineages or a single clonal lineage (Schön et al. 1998, Van Doninck et al.

2002, 2003). This could be due to the challenges associated with assigning individuals to different asexual lineages before genetic studies became standard practice in ecological research. This weakness prevents accurate investigation of the niche breadths of existing clones and may yield misleading patterns where asexual lineages appear to have broad ecological tolerances. In addition, many studies failed to utilise environmental data extracted at sampling sites (Pagano et al. 2008), which prevents researchers from addressing whether geographically widespread asexual clones – that could be first seen as a generalist genotypes – actually occupy a narrow but widely available realised niche. Conversely, when clones are geographically restricted to a few sites (Ellstrand and Roose 1987), it is challenging to ascertain whether this narrow distribution reflects true ecological specialisation, recent emergence from their sexual relatives, or simply a lack of opportunities for dispersal. To overcome all these caveats, empirical approaches aimed at deciphering ecological factors underlying asexual lineage distribution should ideally focus on a cosmopolitan species, wherein asexual lineages are distributed across similar, yet geographically distant, environments and incorporate modern ecological niche approaches.

The study of clonal lineages within the leaf curl plum aphid complex, *Brachycaudus helichrysi* (Hemiptera, Aphididae) fits some of these prerequisites. This worldwide pest species has been recorded in more than 60 countries throughout the Palearctic (Holman 2009) and is also present in the Southern Hemisphere (Blackman and Eastop 2000). As in most aphid species, the typical life cycle of *B. helichrysi* is cyclical parthenogenesis. This involves a sexual reproduction phase occurring in autumn on *Prunus* species (mainly *P. domestica*), resulting in the production of overwintering eggs. Subsequently, an asexual reproduction phase occurs in spring and summer on a large range of herbaceous plants (Bennett 1955, Blackman and Eastop 2000). When biotic and abiotic conditions are favourable during the asexual phase of the aphid cycle, a clone can produce countless number of offspring (i.e. billions of individuals) in a very short time, and rapidly spread. Recent genetic studies have unveiled that *B. helichrysi* is, in fact, a species complex composed of three distinct lineages referred to as H1, H2 and H3 (Piffaretti et al. 2012, 2013a, b, Popkin et al. 2017). Among these lineages, H2 primarily comprises populations that reproduce asexually all year round on herbaceous plants in areas with mild winters (Leather 1992, Piffaretti et al. 2013a). So far, few sexual populations have been identified within H2: these reproduce sexually on peach trees (*P. persica*) and are geographically restricted to northern India and Central Asia (Piffaretti et al. 2013a, Popkin et al. 2017). These geographic locations are characterised by harsh winter conditions that prevent the persistence of asexuality (frost-resistant aphid eggs are necessary for overwintering) (Leather 1992). Within the H2 lineage, eight persistent asexual lineages have been described using microsatellite markers, and experimental studies have confirmed irreversible loss of sexuality in one of these clonal lineages (Piffaretti et al. 2013a). Some of these clones have been found across multiple continents and over

15-year-long stretches (Piffaretti et al. 2013a, Popkin et al. 2017), thereby meeting the definition of aphid superclones (Vorburger et al. 2003a, Figueroa et al. 2018). Published analyses revealed that these clonal lineages do not exhibit significant differences in their associations with host plants at the family and genus level (Piffaretti et al. 2013a). Hence, they do not appear as host-plant specialists as observed, for instance, for *Aphis gossypii* clones (Carletto et al. 2009). Based on these results it may be intuitively assumed that *B. helichrysi* clones are generalist genotypes that can adapt to various environmental conditions. However, the question of putative climatic niche differentiation among aphid superclones, using high-resolution climate data and up-to-date ecological niche analyses, has never been formally addressed. We know from previous research that the distribution of sexual versus asexual lines in aphids is conditioned by climatic conditions in several aphid species (Martel et al. 2020), but within the climatic envelope allowing for the persistence of asexuality, different aphid clones could be associated with different climatic variables.

The aim of this study was to examine whether asexual superclones in the *B. helichrysi* lineage H2 fit this description of ecological generalists or whether they can differ in their climatic niche, and have a narrower niche, which suggests specialisation. To address this question, we used a comprehensive sampling of *B. helichrysi* H2 clones from various locations worldwide. To ensure that we were looking at the aphid genotype adaptation and not a symbiont-driven ecological trait, we first characterised clone association with endosymbiotic bacteria. Indeed, the abiotic niche of arthropods can be greatly influenced by endosymbionts. These can both expand the niche space of their hosts by conferring resistance to factors such as temperature stress (Montllor et al. 2002, Brumin et al. 2011, Burdina et al. 2021), desiccation (Engl et al. 2018), or toxic molecules (Rothman et al. 2019), or restrict it, because of their own set of limitations to abiotic conditions such as extreme heat (Fan and Wernegreen 2013, Kikuchi et al. 2016) or salinity for aquatic organisms (Nougué et al. 2015). Aphid bacterial endosymbionts are known to modulate many aspects of their hosts' ecological niches, including thermal tolerance (Oliver et al. 2010). For instance, it has been shown that two common aphid endosymbionts, *Serratia symbiotica* and *Fukatsuia symbiotica*, can help aphids mitigate the effect of heat stress (Montllor et al. 2002, Russell and Moran 2006, Heyworth and Ferrari 2015, Heyworth et al. 2020, Tougeron et al. 2023). Therefore, it is crucial to identify associations with symbionts when investigating the ecological niches of aphid clonal lineages. The recurrent association of a clone with a particular endosymbiont could indeed lead to a spurious conclusion where the clone appears as a niche specialist though its niche occupancy is driven by the endosymbiont, not the aphid genotype. We then used climatic variables associated with the occurrence data of six globally distributed clones to perform ecological niche divergence analyses. We formally tested whether all clones occur under similar climatic conditions or whether some clones are restricted to specific conditions, showing

little overlap with other clones in their climatic preference. The former would suggest that they are indeed widespread generalists, while the latter would suggest that they are ecological specialists.

## Methods

### Sampling of clones

During the period 1999–2015, we collected over 700 colonies of *B. helichrysi* on 33 host-plant genera in the Americas, Europe, Africa, Asia, and Australia. A colony corresponded to individuals collected from a single plant or, if very few aphids were present, from two neighbouring plants of the same species. Each sampling locality was georeferenced, and the host-plant species was recorded. Full details on sampling methods and specimen conservation are provided in Popkin et al. 2017. Vouchers for these samples (i.e. individuals from the same colonies) can be found in the CBGP arthropod collection (<https://doi.org/10.15454/D6XAKL>) (Coeur d'acier et al. 2014). Among these *B. helichrysi* samples, we selected a subset of individuals that were assigned to six widely distributed H2 clones, based on genotyping using 14 microsatellite markers (Piffaretti et al. 2013a, Popkin et al. 2017) (namely clones 'A', 'B', 'C', 'D', 'F' or 'G' following methods and nomenclature described by Piffaretti et al. 2013a). The final dataset comprised 249 sequenced individuals (clone A: 52 records; clone B: 46 records; clone C: 87 records; clone D: 7 records; clone F: 27 records; and clone G: 30 records) from 10 countries and 163 sampling localities (Fig. 1, Supporting information).

### Characterisation of the endosymbionts associated with each clone

A total of 102 individuals, representative of the six clones and the diversity of their geographic distribution, were used for characterising bacterial endosymbionts (Supporting information). Using DNA extracts from the same individuals utilised for microsatellite genotyping in Piffaretti et al. (2013a) or Popkin et al. (2017), we amplified a 251 bp portion of the V4 region of the 16S rRNA gene (Mizrahi-Man et al. 2013) and used targeted sequencing of indexed bacterial fragments on a MiSeq (Illumina) platform (Kozich et al. 2013) following the protocol described in Jouselin et al. (2016). Each DNA sample was amplified twice (replicates were conducted on distinct 96-well microplates). We also used negative controls (DNA extraction and PCR controls conducted on blank templates) to filter out bacterial contamination during laboratory procedures. A total of 216 PCR products (comprising DNA extracts and controls) were obtained, pooled, and then separated by gel electrophoresis. Bands based on the expected size of the PCR products were excised from the gel, purified with a PCR clean-up and gel extraction kit (Macherey-Nagel), and quantified with the Kapa Library Quantification Kit (Kapa Biosystems).



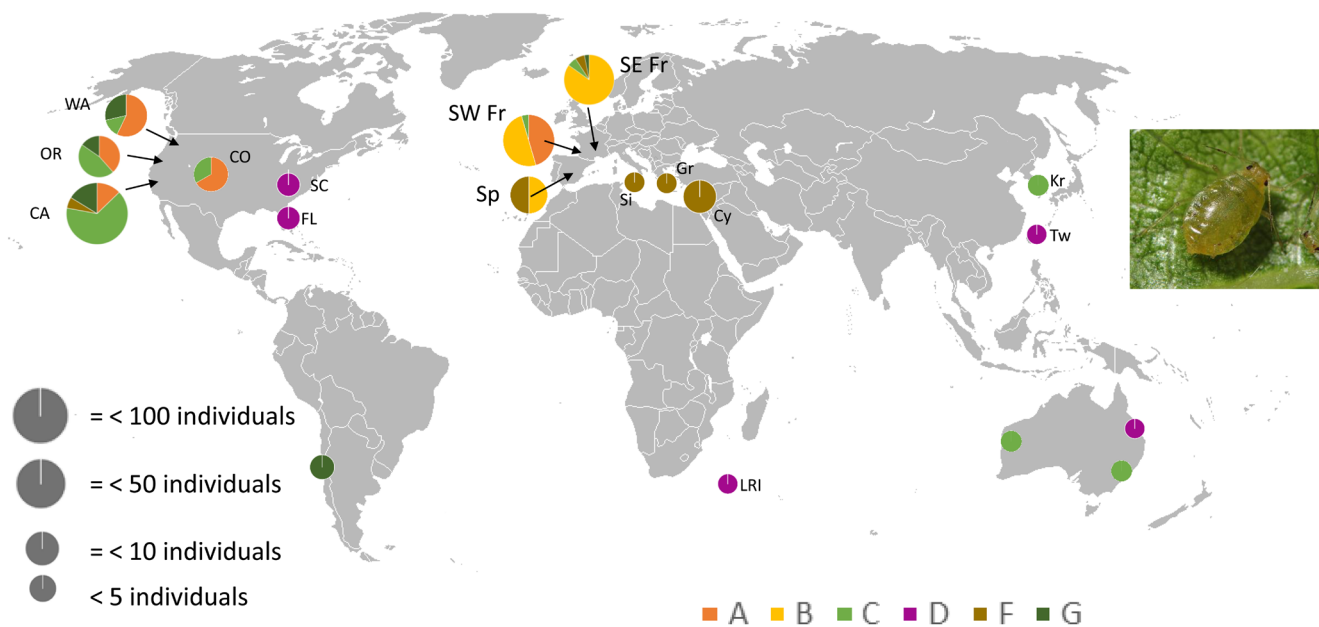


Figure 1. Worldwide distribution of *Brachycaudus helichrysi* superclones. Each clone is represented by a unique colour (refer to the colour legend at the bottom of the map). The size of each pie chart is proportional to the number of occurrences (see legend on the left side of the map) at each sampling site, and the pie chart slices represent the percentage of occurrences of each clone. Abbreviations: WA: Washington State, OR: Oregon, CA: California, CO: Colorado, SC: South Carolina, FL: Florida, Ch: Chile, SW Fr: south-west France, SE Fr: south-east France, Sp: Spain, Si: Sicily, Gr: Greece, Cy: Cyprus, LRI: La Réunion Island France, Kr: Republic of Korea, Tw: Taiwan, QI: Queensland, NSW: New South Wales.

Paired-end sequencing of the DNA pool was carried out on a MISEQ (Illumina) FLOWCELL with a 500-cycle Reagent Kit v2 (Illumina).

We first applied sequence filtering criteria following Illumina's quality control procedure. We then merged paired sequences into contigs with FLASH ver.1.2.11 (Magoč and Salzberg 2011) and trimmed primers with CUTADAPT ver. 1.9.1 (Martin 2011). We then used the FROGS pipeline (Escudíe et al. 2018) to generate an abundance table of symbiont lineages across samples. In brief, we first filtered out sequences > 261 bp and < 241 bp, then we clustered variants into operational taxonomic units (OTUs) with SWARM (Mahé et al. 2014) using a maximum aggregation distance of three. We identified and removed chimeric variants with VSEARCH (Rognes et al. 2016). Taxonomic assignment of OTUs was carried out using RDPtools and Blast (Altschul et al. 1990) against the Silva138-16s database (<https://www.arb-silva.de>) as implemented in FROGS (Escudíe et al. 2018). The resulting abundance table is available in Supporting information. From the abundance table of OTUs across samples, we transformed read numbers per aphid sample into frequencies (percentages); sequences accounting for < 0.5% of all the reads for a given sample were excluded (Jousselin et al. 2016). We then only kept OTUs that were present in both PCR replicates of the same sample. All filters resulted in excluding reads found in low abundance that could represent sequencing errors and which were also often found in the negative controls. Reads that corresponded to OTUs also identified in negative controls were very rare after our filters and did not impact our conclusions.

## Realised climatic niche divergence

### Distributional data and bioclimatic descriptors

We investigated realised climatic niche divergence among *B. helichrysi* clones by extracting values of 20 ecologically relevant bioclimatic variables from each sampling locality. Bioclimatic data were obtained from the CHELSA database at a resolution of 30 arc-seconds (Karger et al. 2017). These bioclimatic data represent worldwide historical trends in temperature, solar radiation, and precipitation for the period 1979–2013 (Supporting information). For each clone, we removed duplicated records, i.e. we only allowed one occurrence per pixel of the bioclimatic rasters. After removing duplicated records, the presence dataset encompassed 176 occurrences (Table 1).

### Niche equivalency tests

We employed niche equivalency tests to examine the divergence in climatic niches among clones (Broennimann et al. 2012). The analysis was conducted using the 'ade4' package (Dray and Dufour 2007) and the 'ecospat' package (Di Cola et al. 2017) in R ([www.r-project.org](http://www.r-project.org)). We compared the niches of clones in a bidimensional space defined by a between-class analysis (BCA) (Dolédec and Chessel 1987), calibrated on the entire environmental space represented by climatic values associated with the occurrences of all clones of *B. helichrysi* H2. The BCA – namely the 'BETWEEN-occ' approach according to Broennimann et al. (2012) – was preferred to other ordination approaches because this technique maximises both inter-individual and between-classes (here, the different clones) variance, aligning with the objective of

Table 1. Number of occurrences included in the analyses after removing duplicated occurrences and results of the climatic niche equivalency tests derived from both between-class analyses (i.e. BCA#1: clone D versus all other clones; BCA#2: each clone compared to other clones excluding the clone D).

Clone	Number of occurrences	Observed Schoener's D index	Niche equivalency test p values	Analysis
Clone A	34	0.52	0.005	BCA #2
Clone B	35	0.14	0.001	BCA #2
Clone C	56	0.53	0.001	BCA #2
Clone D	6	0.06	0.052	BCA #1
Clone F	19	0.48	0.013	BCA #2
Clone G	26	0.59	0.037	BCA #2

the study. To assess niche equivalency, we performed subsequent tests comparing the niche of each clone against the collective niche of all other remaining clones, employing niche equivalency test based on Schoener's D index (Schoener 1968). We opted for a resolution of  $100 \times 100$  when creating the grid with occurrence densities along gridded environmental gradients. Occurrence data for all clones were then 1000 times combined and randomly allocated to two datasets of the same size as the dataset under investigation (number of occurrences for the clone being examined versus the number of remaining occurrences). We compared the observed D values between clonal lineages to the distribution of these 1000 simulated values. If the observed D fell within the density of 95% simulated values, the null hypothesis – indicating niche equivalency – could not be rejected.

Outputs of this first BCA (referred to as BCA #1 in the following text) suggested that clone D, which occurs in tropical and sub-tropical regions, may have a substantially different climatic envelope compared to all other clones, which by contrast occur in temperate regions. Capturing subtle niche differences between most temperate clones (i.e. all clones except clone D) was thus challenging in this factorial bidimensional BCA-derived environmental space. Indeed, the climatic variables with the highest loading scores on both first factorial axes of the BCA #1 mainly reflect the duality between tropical versus temperate climates and could be unsuited to uncover differences between temperate clones. To capture differences between temperate clones, we thus repeated the full procedure while excluding clone D (referred to as BCA #2 in the following text). In this BCA #2 approach, the BCA was calibrated on the entire environmental space represented by climatic values associated with the occurrences of *B. helichrysi* lineage H2, all clones included except clone D.

## Results

### Diversity of endosymbionts associated with *B. helichrysi* clones

After sequence filtering steps, the high-throughput sequencing of 16S rRNA bacterial genes of 102 aphids and six negative controls resulted in 3 million sequencing reads with an

average of 13 680 reads per PCR product. After the application of all necessary filters to remove contaminants, the remaining dataset consisted of 2.7 million sequencing reads, which were clustered into 55 OTUs. This survey revealed a low diversity of bacterial symbionts in *B. helichrysi* clones (Supporting information). Most of the reads (75%) were assigned to the aphid primary symbiont *Buchnera aphidicola* which was found, as expected, in all samples. Another well-known aphid endosymbiont, *H. defensa*, accounted for 3.5% of the reads and was found in 21 out of the 102 aphid specimens. A single sample contained another known aphid endosymbiont, *Erwinia haradae* (Manzano-Marín et al. 2020). Other samples did not host any common aphid endosymbionts. The remaining sequencing reads were either assigned to ubiquitous bacteria (that were sometimes not assigned below family level, such as Chitinophagaceae), or represented bacteria found at very low frequencies, i.e. below 0.5% of the reads in the samples (these are represented in grey in the Supporting information). These bacteria might therefore be biologically irrelevant. Overall, the analysis indicated a scarcity of symbionts associated with *B. helichrysi* individuals, regardless of their clonal lineage. The endosymbiont *H. defensa* was predominantly found in clone C (it was found in 26%, 48%, and 7% of individuals belonging to clones B, C and F, respectively (Supporting information).

### Ecological niche divergence between asexual lineages

#### Climatic niche divergence analyses

The results of BCA #1 are presented graphically in Fig. 2. The first two factorial axes of the BCA #1 accounted for 61.4 and 20.1 % of the total variation in climate conditions experienced by the clones, respectively. In the BCA #1, the first factorial axis clearly distinguished clone D from all other clones (Fig. 2). Clone D is associated with high annual precipitation (bio12), and high amounts of precipitation during the driest and the warmest periods of the year (bio14, bio17, bio18). Clone D is also associated with high temperature during the coldest, warmest, and wettest periods of the year (bio5, bio6, bio8), high annual mean temperature (bio1) and low values of mean diurnal range (bio2), isothermality (bio3), and precipitation seasonality (bio15) (Fig. 2). The hypothesis of niche equivalency between clone D and all other clones combined was close to being rejected; Table 1, Supporting information). The limited sample size of clone D (only six records, albeit from distant sites as shown in Fig. 1) may explain the marginal significance despite the distinct position of clone D in the BCA #1 analysis (Table 1).

Graphical outputs of the BCA #2 calibrated without considering clone D (correlation circles and score plots) are given in Fig. 3. The first two BCA #2 axes accounted for 65.2 and 25.3 % of the total variation in climate conditions experienced by the clones, respectively. Based on the BCA #2, the hypothesis of niche equivalency between clones was rejected for each clone (Table 1, Supporting information). The first BCA #2 factorial axis strongly discriminates clone

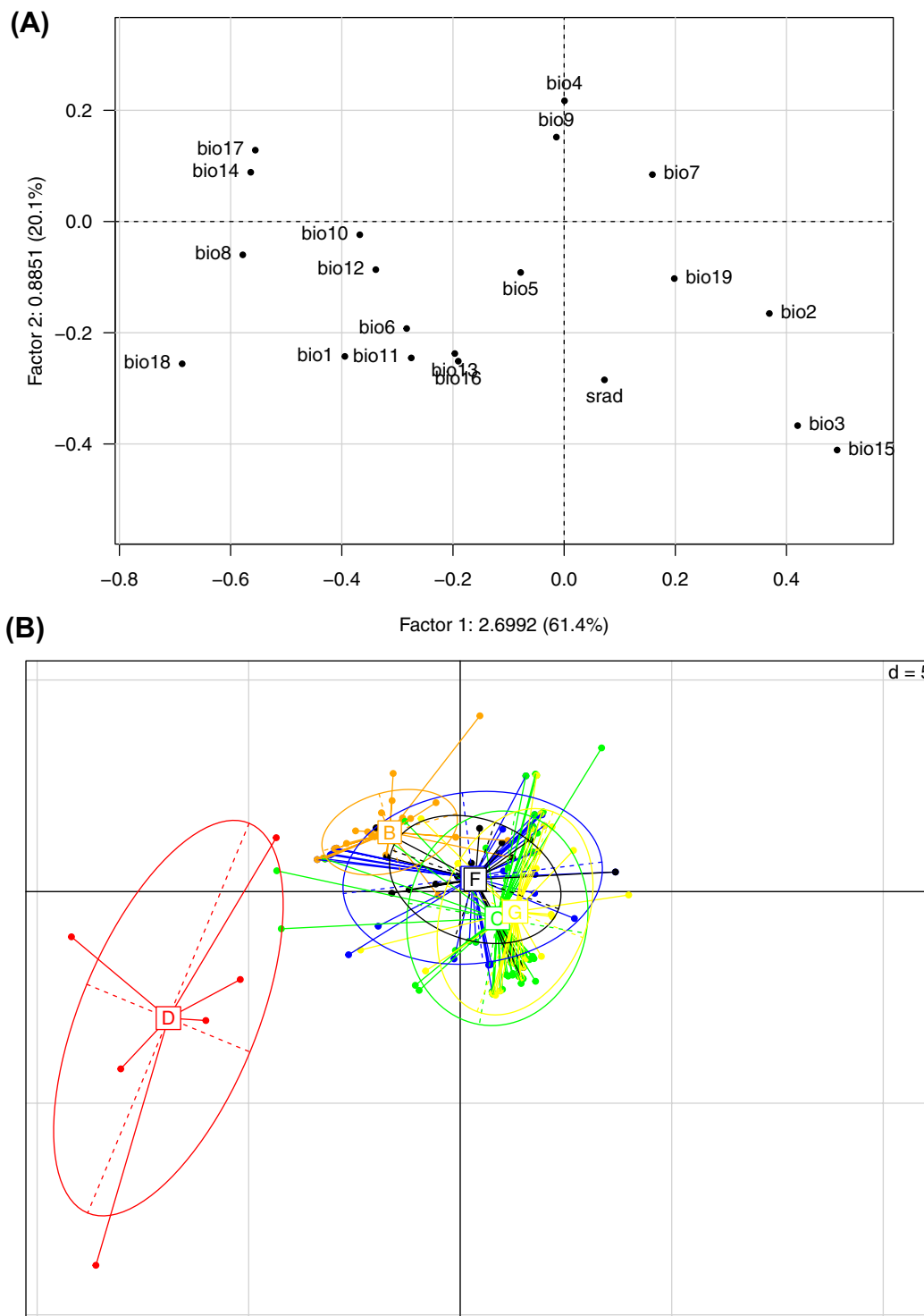


Figure 2. (A) Scores of bioclimatic variables on the first two factorial axes of the between-class analysis #1 (i.e. all clones included). See Supporting information for explanation of abbreviations of climatic variables. (B) Position of six *Brachycaudus helichrysi* clones (i.e. clones A, B, C, D, F and G) along the two first axes of this between-class analysis #1.

B from all other clones (Fig. 3). Clone B is associated with relatively high amounts of precipitation during the driest and warmest period of the year (bio14, bio17, bio18), high temperature during the wettest quarter of the year (bio8), low

isothermality (bio3), and low rainfall seasonality (bio15) (Fig. 3). Clone A has a positive score on the second BCA #2 factorial axis (Fig. 3). The niche position of clone A is associated with high diurnal range (bio2), low annual solar

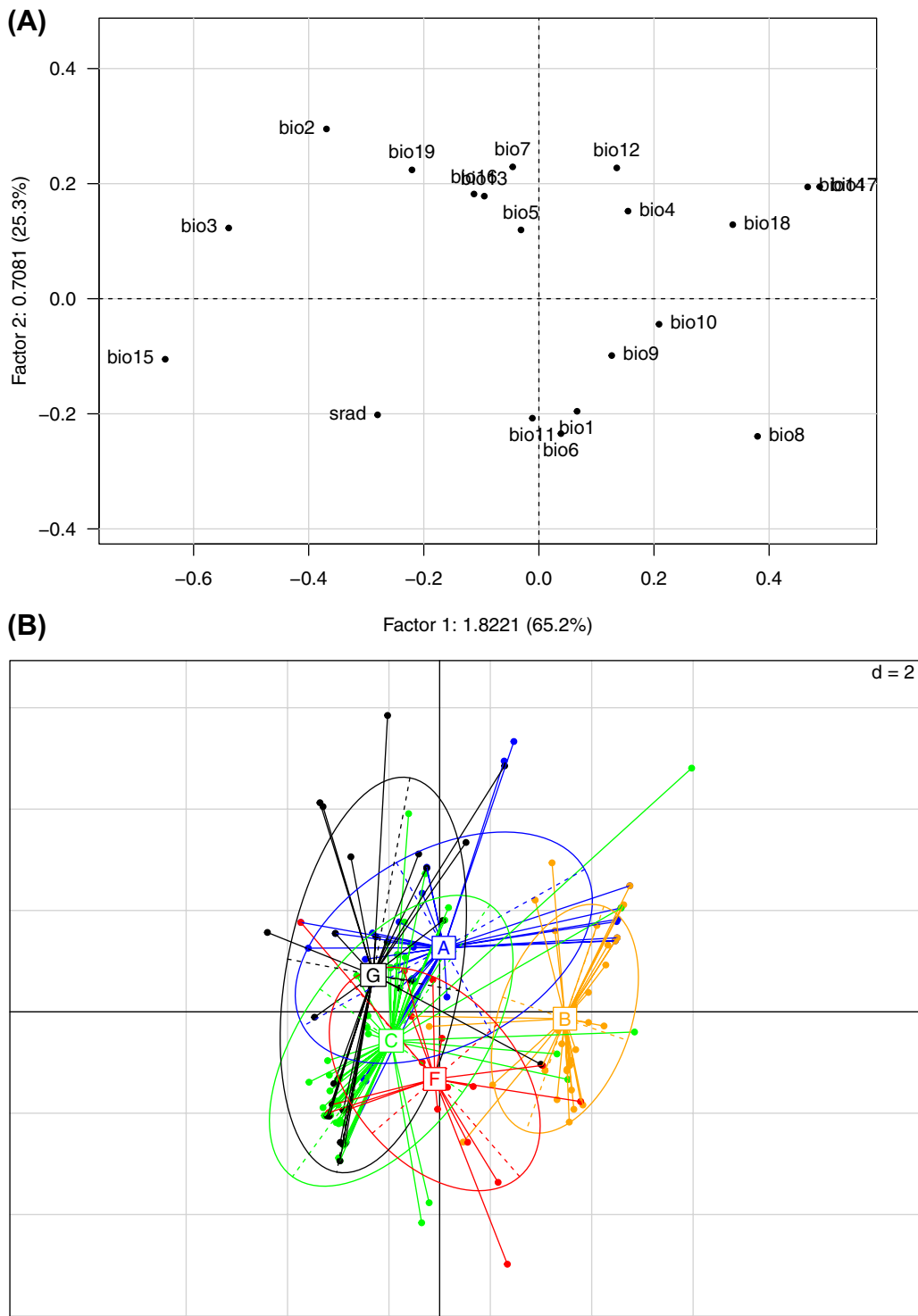


Figure 3. (A) Scores of bioclimatic variables on the first two factorial axes of the between-class analysis #2 (i.e. all clones included except clone D). See Supporting information for explanation of abbreviations of climatic variables. (B) Position of five *Brachycaudus helichrysi* clones (i.e. clones A, B, C, F and G) along the two first axes of this between-class analysis #2.

radiation, a cold winter (bio6, bio11), high annual temperature range (bio7), low annual average temperature (bio1), and high amounts of precipitation during the coldest quarter of the year (bio19) (Fig. 3). Clone C has a negative score on

the first BCA #2 factorial axis (Fig. 3). This reflects a niche position associated with relatively low amounts of precipitation during the driest and warmest period of the year (bio14, bio17, bio18), low temperature during the wettest quarter of



the year (bio8), high isothermality (bio3), and high rainfall seasonality (bio15) (Fig. 3). Clone F occupies a negative position on the second BCA #2 factorial axis (Fig. 3). The niche position of clone F on the BCA #2 factorial space is associated with low diurnal range (bio2), high solar radiation and warm and dry winter (bio6, bio11, bio19), and high temperature during the wettest quarter of the year (bio8) (Fig. 3). The niche position of clone G is associated with high diurnal range (bio2), isothermality (bio3) and precipitation seasonality (bio15), low temperatures during the wettest period of the year (bio8), and relatively low amounts of precipitations during the driest and warmest period of the year (bio14, bio17, bio18) (Fig. 3).

## Discussion

Understanding the ecological differentiation of asexual lineages provides valuable insights into the maintenance and evolutionary dynamics of asexuality, shedding light on the factors driving clones' geographic distributions and ecological success. Aphids yield persistent clonal lineages that can expand over large geographic scales, sometimes over continents. Among the aphid species that comprise such lineages are *Myzus persicae* (Vorburger et al. 2003a), *Sitobion avenae* (Figueroa et al. 2005), *Aphis gossypii* (Carletto et al. 2009), *B. helichrysi* (Piffaretti et al. 2013a), and *Melanaphis sacchari* (Nibouche et al. 2014). Because of their wide distribution and apparent ecological success, these so-called superclones are intuitively assumed to be generalist genotypes that show a high degree of phenotypic plasticity and therefore adaptability to various environments (Haack et al. 2000, Figueroa et al. 2005, 2018). This adaptability can refer to their host-plant associations, but also to other biotic factors such as resistance to various natural enemies (Ferrari et al. 2001). Until now, the breadth of their climatic tolerance has actually been seldom investigated among aphid clones. Taking advantage of a worldwide sampling of *B. helichrysi* and using multivariate ecological niche analyses, we provide here evidence that aphid superclones are not generalists with respect to their climatic tolerance. We reveal significant differentiation in the realised climatic niche of six *B. helichrysi* superclones. Though it was represented by few occurrences, we found potential niche specialisation of one clone (clone D) to tropical or subtropical climatic conditions (Fig. 2, Table 1). The remaining clones were found in geographic areas characterised by temperate climatic conditions but showed some specificity within this range (Fig. 3). For instance, clone F was clearly restricted to the Mediterranean-climate regions, while clones A and B showed apparent niche specialisation to colder temperate climates. Hence, despite their large geographic distributions, *B. helichrysi* superclones do not seem to fit the generalist genotype definition, and the 'super' in superclones might refer to being better at exploiting a specific niche.

A few previous studies had also refuted the assumptions that aphid clonage lineages were ecological generalists. For instance, it has been shown that, in both *Aphis gossypii*

and *Melanaphis sorghi* (formerly thought to be *M. sacchari*; Nibouche et al. 2021), long-term asexual lineages have distinct sets of preferred host plants (Carletto et al. 2009, Nibouche et al. 2015). Some clonal lineages of *Acyrtosiphon pisum* that have spread from Europe to South America also appear to be specialised on specific host plants (Peccoud et al. 2008). Studies of *S. avenae* showed that though clonal lineages were highly plastic in their feeding behaviour (Barrios-SanMartín et al. 2016), they could be characterised by different resistance to insecticides (Figueroa et al. 2004, Castañeda et al. 2010), also suggesting some type of clone niche specialisation. On the other hand, *M. persicae* clones appear as highly generalist regarding their host-plant use (Fenton et al. 2005), and the molecular determinants of this extreme plasticity have been uncovered (Mathers et al. 2017). However, using experimental approaches, it was shown that *M. persicae* clones found in Australia did not have a better mean fitness across diverse plants when compared to their sexual counterparts (Vorburger et al. 2003b). Hence, generalism towards host-plant use is not a characteristic of clonality in this species (Vorburger et al. 2003b). Also, Medina et al. (2017) showed that *M. sacchari* occurring in the USA belongs to three genetically distinct entities. However, these clusters were not associated to any different specific host plant or geographic association. To our knowledge, the present study is the first one that presents evidence for aphid superclones' adaptation to climate conditions. Beyond studies of superclone niche occupancy, this is also the first evidence that, within a cosmopolitan aphid species, distinct lineages can have a preferred set of climatic conditions. Aphid 'biotypes' are generally designated based on biological characteristics such as different sets of host plants but, to our knowledge, there are no studies showing that aphid biotypes differ in their climatic tolerance. Gilabert et al. (2015) had previously suggested that climatic specialisation of aphid clones was possible, as they showed that two clonal lineages of *Rhopalosiphum padi* exhibited different geographical clines. However, their analysis was restricted to northern France and did not include any statistical analyses of climatic variables.

The signal of climatic differentiation detected in our study is robust. First, we sampled *B. helichrysi* H2 populations in five continents and across a wide range of climatic conditions and, therefore, we likely have captured well the realised climatic niche of this lineage. Second, we found similar patterns of climatic niche occupation in spatially independent biogeographic areas for several clones. For example, clone D was consistently found in tropical and subtropical climates in four biogeographic regions, i.e. Australia, Asia, North America and Indian Ocean islands (Fig. 1). Similarly, clone F, which mainly occurs in the Mediterranean basin, was also collected in a similar Mediterranean-climate habitat in the USA (i.e. California, Fig. 1). This suggests that the signals of niche specialisation are not due to dispersal limitations of these clones. The disjunct distribution of most clones is striking. It agrees with previous studies that show that some common aphid pests are regularly transported across the globe through human activities (Margaritopoulos et al. 2009).

Regarding more particularly our study system, *B. helichrysi*, some of their typical host plants are *Chrysanthemums*, that are known to be traded intensively across the globe. Given the spread of some clones (up to four continents for clone C and clone D), we can anticipate that all *B. helichrysi* clones are regularly transported across continents on potted plants and the resulting distribution is a product of environmental filters that select for adapted genotypes. Alternative explanations for such a signal of aphid genotype–climate associations not involving climatic adaptation of the insects, would imply that the transcontinental trades of common ornamental plants only occur between areas with similar climates. This latter hypothesis seems highly unlikely and further legitimates using the entire environmental space defined by all clones' occurrences as the background region for each clone in niche equivalency tests. The signal of climatic niche specialisation is also unlikely to be due to biotic associations (e.g. association of clones with specific host plants or natural enemies) limiting each clone's geographic range, as similar biotic conditions are unlikely to be replicated between distant sites. In agreement with this assumption, it was shown that there were no significant differences between host-plant ranges among clones of *B. helichrysi* (Piffaretti et al. 2013a).

Finally, we found a low diversity of facultative bacterial endosymbionts in sampled specimens, with a majority of specimens (80%) that hosted no symbiont apart from *B. aphidicola*. The endosymbiont *S. symbiotica* that is known to play a role in aphids' resistance to heat stress (Montllor et al. 2002, Tougeron et al. 2023) was not found in any of our samples, not even in samples of clone F, which is specifically found in areas characterised by hot summers. Hence, altogether this suggests that associations with facultative endosymbionts do not play a role in clone niche occupancy. The only recurrent associations found in our study was the one of *H. defensa* with clone B and C. This symbiont is known to induce resistance to parasitoids (Vorburger 2014). Therefore, it is very unlikely that it is *H. defensa* that drives clones' climatic niche occupancy. Elucidating why *H. defensa* is repeatedly found in clones B and C but not in other clones is beyond the scope of this paper.

As stated in the introduction, the ecological factors underlying distribution of clonal lineages have been explored in different organisms, with studies showing that long-term asexuals can be either generalists or specialists depending on biological systems (Vrijenhoek and Parker 2009). Since this thorough review paper, among studies on arthropods, recent work on *Timema* stick insects has shown that clonal lineages exhibit narrower realised niches than their sexual relatives (Larose et al. 2018), and studies on water fleas have demonstrated that clonal composition of populations is structured by environmental variables (Groot et al. 2005, Pantel et al. 2011, Haileeslasie et al. 2016). Both of these examples suggest to some extent that asexual lines tend to be ecological specialists. On the other hand, in ambrosia beetles, two clonal lineages show very similar niche occupancy in terms of host-plant utilisation (Andersen et al. 2012). Also, in asexual *Daphnia*, the invasion and dominance of a single clone has

been observed in several lakes throughout a wide geographic range and broad environmental conditions (Dane et al. 2020). Among empirical approaches that compare the geographical distribution of different clonal lineages, few have employed statistical investigations of climatic factors underlying these distributions, and none have focused on arthropod species. Coughlan et al. (2017) found clonal lineages in hawthorns with large ecological tolerances fitting the generalist clone hypothesis; while Greenwald et al. (2016), on the other hand, found significant climatic niche differentiation among unisexual lineages of *Ambystoma* salamanders. But in many species that encompass asexual lineages, when these lineages expand over large geographic areas, they are often assumed to be generalists without further analyses of environmental variables behind their distribution. This is the case in oribatid mites (Maraun et al. 2022) where geographic range sizes have been explicitly used as a proxy for specialisation. In this system, conclusions regarding asexual lineages' generalist ecological strategy have been drawn from their large range sizes but this was solely based on range size comparison of sexual and asexual populations. In aphids, though the climatic envelope of asexual lines is narrower than the one of sexual lines (as it is limited to areas with overall low seasonality and mild or warm winters), we show here that there are finer variations to which clonal genotypes might be adapted. Before concluding that climatic adaptation is completely endogenous (i.e. solely the product of the aphid genotype), it might also be interesting to investigate the *Buchnera* strains that are associated with *B. helichrysi* clonal lineages. Indeed, it has been demonstrated that the obligate symbiont *B. aphidicola* can differ in a gene coding for a heat-shock protein (Zhang et al. 2019), which then helps aphids resist temperature stress. Genetic variations in *Buchnera* might therefore also play a role in determining abiotic niche occupancy.

## Conclusions

The present study provides evidence for intraspecific climatic niche divergence in a cosmopolitan aphid species, which is not mediated by associations with facultative endosymbionts. It suggests that ecological specialisation towards climatic variables in *B. helichrysi* clones shapes the geographic areas they can occupy. To our knowledge, climatic adaptation has seldom been hypothesised to underlie the spatial distribution of intraspecific genetic diversity in aphids, the host plants having been seen as the main factors explaining their phylogeographic distributions (Nikolakakis et al. 2003, Peccoud et al. 2008, Carletto et al. 2009, Nibouche et al. 2015). This study adds to the evidence that aphid lineages can have their own set of climatic limitations beyond the availability of suitable host plants (Arnal et al. 2019). Despite the significant signal observed in our study, correlative distribution-based ecological niche analyses must always be interpreted guardedly (Peterson et al. 2011) since they only depict the realised niche, i.e. a subset of the full range of environmental conditions suitable for a taxon (Hutchinson 1957). Therefore, the adaptation of *B. helichrysi*

superclones to climatic conditions needs to be confirmed with experimental approaches manipulating temperature and humidity in controlled laboratory conditions. Altogether, the presence of some clones in more than three continents, despite their specialisation, is a testimony of the intensity of human-mediated long-distance dispersal events at a global scale. If clonal genotypes were ecological generalists, we could expect that they have expanded by natural dispersal, surviving along the way through non-preferred environments. Our results rather suggest repeated multiple human-mediated long-dispersal introduction events and subsequent environmental filtering (i.e. local selection of climatically adapted clones).

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## Author contributions

**Martin Godefroid:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Writing – original draft (lead); Writing – review and editing (lead). **Christine N. Meynard:** Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Investigation (equal); Methodology (equal); Supervision (equal); Writing – review and editing (equal). **Anne-Laure Clamens:** Data curation (equal). **Megan Popkin:** Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Writing – review and editing (equal). **Emmanuelle Joussetin:** Data curation (equal); Formal analysis (equal); Funding acquisition (lead); Investigation (lead); Methodology (equal); Project administration (lead); Supervision (lead); Writing – original draft (equal); Writing – review and editing (equal).

## Data availability statement

Information on sampling is available in the database <https://aphiddb.supagro.inrae.fr/>.

Data are available from the Zenodo Digital Repository: <https://zenodo.org/records/10924797> (Joussetin and Godefroid 2024).

## Supporting information

The Supporting information associated with this article is available with the online version.

## References

- Altschul, S. F., Gish, W., Miller, W., Myers, E. W. and Lipman, D. J. 1990. Basic local alignment search tool. – *J. Mol. Biol.* 215: 403–410.
- Andersen, H. F., Jordal, B. H., Kambestad, M. and Kirkendall, L. R. 2012. Improbable but true: the invasive inbreeding ambrosia beetle *Xylosandrus morigerus* has generalist genotypes. – *Ecol. Evol.* 2: 247–257.
- Arnal, P., Coeur d’acier, A., Favret, C., Godefroid, M., Qiao, G.-X., Joussetin, E. and Sanchez Meseguer, A. 2019. The evolution of climate tolerance in conifer-feeding aphids in relation to their host’s climatic niche. – *Ecol. Evol.* 9: 11657–11671.
- Baker, H. G. 1965. Characteristics and modes of origin of weeds. – In: Baker, H. G. and Stebbins, G. L. (eds), *The genetics of colonizing species*. Academic Press, pp. 147–168.
- Barrios-SanMartín, J., Figueroa, C. C. and Ramírez, C. C. 2016. Evidence of plastic probing behavior in a ‘superclone’ of the grain aphid *Sitobion avenae*. – *Bull. Entomol. Res.* 106: 801–808.
- Bell, G. 1982. The paradox of sexuality. – In: Bell, G. (ed.), *The masterpiece of nature: the evolution and genetics of sexuality*. Univ. of California Press, pp. 160–331.
- Bennett, S. H. 1955. The biology, life history and methods of control of the leaf curling plum aphid *Brachycaudus helichrysi* (Kltb.). – *J. Hortic. Sci.* 30: 252–259.
- Blackman, R. L. and Eastop, V. F. 2000. *Aphids on the world’s crops: an identification and information guide*. – John Wiley & Sons Ltd.
- Broennimann, O., Fitzpatrick, M. C., Pearman, P. B., Petitpierre, B., Pellissier, L., Yoccoz, N. G., Thuiller, W., Fortin, M.-J., Randin, C., Zimmermann, N. E., Graham, C. H. and Guisan, A. 2012. Measuring ecological niche overlap from occurrence and spatial environmental data. – *Global. Ecol. Biogeogr.* 21: 481–497.
- Brumin, M., Kontsedalov, S. and Ghanim, M. 2011. *Rickettsia* influences thermotolerance in the whitefly *Bemisia tabaci* B biotype. – *Insect Sci.* 18: 57–66.
- Burdina, E. V., Bykov, R. A., Menshanov, P. N., Ilinsky, Y. Y. and Gruntenko, N. E. 2021. Unique *Wolbachia* strain wMelPlus increases heat stress resistance in *Drosophila melanogaster*. – *Arch. Insect Biochem. Physiol.* 106: e21776.
- Carletto, J., Lombaert, E., Chavigny, P., Brévault, T., Lapchin, L. and Vanlerberghe-Masutti, F. 2009. Ecological specialization of the aphid *Aphis gossypii* Glover on cultivated host plants. – *Mol. Ecol.* 18: 2198–2212.
- Castañeda, L. E., Figueroa, C. C., Fuentes-Contreras, E., Niemeyer, H. M. and Nespole, R. F. 2010. Physiological approach to explain the ecological success of ‘superclones’ in aphids: interplay between detoxification enzymes, metabolism and fitness. – *J. Insect Physiol.* 56: 1058–1064.
- Coeur d’Acier, A., Cruaud, A., Artige, E., Genson, G., Clamens, A. L., Pierre, E., Hudaverdian, S., Simon, J. C., Joussetin, E. and Rasplus, J. Y. 2014. DNA barcoding and the associated PhylAphidB@ se website for the identification of European aphids (Insecta: Hemiptera: Aphididae). – *PLoS One* 9: e97620.
- Coughlan, J. M., Han, S., Stefanović, S. and Dickinson, T. A. 2017. Widespread generalist clones are associated with range and niche expansion in allopolyploids of Pacific northwest hawthorns (*Crataegus* L.). – *Mol. Ecol.* 26: 5484–5499.
- Dane, M., Anderson, N. J., Osburn, C. L., Colbourne, J. K. and Frisch, D. 2020. Centennial clonal stability of asexual *Daphnia* in Greenland lakes despite climate variability. – *Ecol. Evol.* 10: 14178–14188.
- Di Cola, V., Broennimann, O., Petitpierre, B., Breiner, F. T., d’Amen, M., Randin, C., Engler, R., Pottier, J., Pio, D., Dubuis, A., Pellissier, L., Mateo, R. G., Hordijk, W., Salamin, N. and



- Guisan, A. 2017. ecospat: an R package to support spatial analyses and modeling of species niches and distributions. – *Ecography* 40: 774–787.
- Dolédéc, S. and Chessel, D. 1987. Rythmes saisonniers et composantes stationnelles en milieu aquatique. I: Description d'un plan d'observation complet par projection de variables. – *Acta Oecol. Oecol. Gen.* 8: 403–426.
- Dray, S. and Dufour, A.-B. 2007. The ade4 package: implementing the duality diagram for ecologists. – *J. Stat. Softw.* 22: 1–20.
- Ellstrand, N. C. and Roose, M. L. 1987. Patterns of genotypic diversity in clonal plant species. – *Am. J. Bot.* 74: 123–131.
- Engl, T., Eberl, N., Gorse, C., Krüger, T., Schmidt, T. H. P., Plarre, R., Adler, C. and Kaltenpoth, M. 2018. Ancient symbiosis confers desiccation resistance to stored grain pest beetles. – *Mol. Ecol.* 27: 2095–2108.
- Escudí, F., Auer, L., Bernard, M., Mariadassou, M., Cauquil, L., Vidal, K., Maman, S., Hernandez-Raquet, G., Combes, S. and Pascal, G. 2018. FROGS: find, rapidly, OTUs with galaxy solution. – *Bioinformatics* 34: 1287–1294.
- Fan, Y. and Wernegreen, J. J. 2013. Can't take the heat: high temperature depletes bacterial endosymbionts of ants. – *Microb. Ecol.* 66: 727–733.
- Fazlioglu, F. and Bonser, S. P. 2016. Phenotypic plasticity and specialization in clonal versus non-clonal plants: a data synthesis. – *Acta Oecol.* 77: 193–200.
- Fenton, B., Malloch, G., Woodford, J. A. T., Foster, S. P., Anstead, J., Denholm, I., King, L. and Pickup, J. 2005. The attack of the clones: tracking the movement of insecticide-resistant peach-potato aphids *Myzus persicae* (Hemiptera: Aphididae). – *Bull. Entomol. Res.* 95: 483–494.
- Ferrari, J., Müller, C. B., Kraaijeveld, A. R. and Godfray, H. C. J. 2001. Ferrari, J., Müller, C. B., Kraaijeveld, A. R. and Godfray, H. C. J. 2001. Clonal variation and covariation in aphid resistance to parasitoids and a pathogen. – *Evolution* 55: 1805–1814.
- Figueroa, C. C., Fuentes-Contreras, E., Molina-Montenegro, M. A. and Ramírez, C. C. 2018. Biological and genetic features of introduced aphid populations in agroecosystems. – *Curr. Opin. Insect Sci.* 26: 63–68.
- Figueroa, C. C., Simon, J. C., Le Gallic, J. F., Prunier-Leterme, N., Briones, L. M., Dedryver, C. A. and Niemeyer, H. M. 2005. Genetic structure and clonal diversity of an introduced pest in Chile, the cereal aphid *Sitobion avenae*. – *Heredity (Edinb)* 95: 24–33.
- Figueroa, C. C., Simon, J. C., Le Gallic, J. F., Prunier-Leterme, N., Briones, L. M., Dedryver, C. A. and Niemeyer, H. M. 2004. Effect of host defense chemicals on clonal distribution and performance of different genotypes of the cereal aphid *Sitobion avenae*. – *J. Chem. Ecol.* 30: 2515–2525.
- Gilbert, A., Dedryver, C. A., Stoeckel, S., Plantegenest, M. and Simon, J. C. 2015. Longitudinal clines in the frequency distribution of 'super-clones' in an aphid crop pest. – *Bull. Entomol. Res.* 105: 694–703.
- Greenwald, K. R., Denton, R. D. and Gibbs, H. L. 2016. Niche partitioning among sexual and unisexual *Ambystoma* salamanders. – *Ecosphere* 7: e01579.
- Groot, T. V. M., Janssen, A., Pallini, A. and Breeuwer, J. A. J. 2005. Adaptation in the asexual false spider mite *Brevipalpus phoenicis*: evidence for frozen niche variation. – *Exp. Appl. Acarol.* 36: 165–176.
- Haack, L., Simon, J. C., Gauthier, J. P., Plantegenest, M. and Dedryver, C. A. 2000. Evidence for predominant clones in a cyclically parthenogenetic organism provided by combined demographic and genetic analyses. – *Mol. Ecol.* 9: 2055–2066.
- Haileselassie, T. H., Mergeay, J., Weider, L. J., Sommaruga, R., Davidson, T. A., Meerhoff, M., Arndt, H., Jürgens, K., Jeppesen, E. and De Meester, L. 2016. Environment not dispersal limitation drives clonal composition of Arctic *Daphnia* in a recently deglaciated area. – *Mol. Ecol.* 25: 5830–5842.
- Heyworth, E. R. and Ferrari, J. 2015. A facultative endosymbiont in aphids can provide diverse ecological benefits. – *J. Evol. Biol.* 28: 1753–1760.
- Heyworth, E. R., Smee, M. R. and Ferrari, J. 2020. Aphid facultative symbionts aid recovery of their obligate symbiont and their host after heat stress. – *Front. Ecol. Evol.* 8: 56.
- Holman, J. 2009. Host plant catalog of aphids. – Springer Netherlands.
- Hutchinson, G. E. 1957. Concluding remarks. – *Cold Spring Harbor Symposium on Quantitative Biology* 22: 415–427.
- Tougeron, K., Iltis, C., Rampnoux, E., Goerlinger, A., Dhondt, L. and Hance, T. 2023. Still standing: the heat protection delivered by a facultative symbiont to its aphid host is resilient to repeated thermal stress. – *Curr. Res. Insect Sci.*: 100061.
- Jousselin, E. and Godefroid, M. 2024. 16S rDNA sequencing data for characterizing the endosymbionts of leaf curl plum aphid (*Brachycaudus helichrysi*) clones. – Zenodo Digital Repository, <https://zenodo.org/records/10924797>.
- Jousselin, E., Clamens, A.-L., Galan, M., Bernard, M., Maman, S., Gschloessl, B., Dupont, G., Meseguer, A. S., Calevro, F. and Coeur D'Acier, A. 2016. Assessment of a 16S rRNA amplicon Illumina sequencing procedure for studying the microbiome of a symbiont-rich aphid genus. – *Mol. Ecol. Resour.* 16: 628–640.
- Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Keft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P. and Kessler, M. 2017. Climatologies at high resolution for the earth's land surface areas. – *Sci. Data* 4: 170122.
- Kikuchi, Y., Tada, A., Musolin, D. L., Hari, N., Hosokawa, T., Fujisaki, K. and Fukatsu, T. 2016. Collapse of insect gut symbiosis under simulated climate change. – *mBio* 7: e01578–16.
- Kozich, J. J., Westcott, S. L., Baxter, N. T., Highlander, S. K. and Schloss, P. D. 2013. Development of a dual-index sequencing strategy and curation pipeline for analyzing amplicon sequence data on the MiSeq Illumina sequencing platform. – *Appl. Environ. Microbiol.* 79: 5112–5120.
- Larose, C., Parker, D. J. and Schwander, T. 2018. Fundamental and realized feeding niche breadths of sexual and asexual stick insects. – *Proc. R. Soc. B* 285: 20181805.
- Leather, S. R. 1992. Aspects of aphid overwintering (Homoptera: Aphidinea: Aphididae). – *Entomol. Gen.* 17: 101–113.
- Lynch, M. 1984. Destabilizing hybridization, general-purpose genotypes and geographic parthenogenesis. – *Q. Rev. Biol.* 59: 257–290.
- Magoč, T. and Salzberg, S. L. 2011. FLASH: fast length adjustment of short reads to improve genome assemblies. – *Bioinformatics* 27: 2957–2963.
- Mahé, F., Rognes, T., Quince, C., de Vargas, C. and Dunthorn, M. 2014. Swarm: robust and fast clustering method for amplicon-based studies. – *PeerJ* 2: e593.
- Manzano-Marín, A., Coeur d'acier, A., Clamens, A. L., Orvain, C., Cruaud, C., Barbe, V. and Jousselin, E. 2020. Serial horizontal transfer of vitamin-biosynthetic genes enables the establishment of new nutritional symbionts in aphids' di-symbiotic systems. – *ISME J.* 14: 259–273.
- Maraun, M., Bischof, P. S. P., Klemp, F. L., Pollack, J., Raab, L., Schmerbach, J., Schaefer, I., Scheu, S. and Caruso, T. 2022. "Jack-of-all-trades" is parthenogenetic. – *Ecol. Evol.* 12: e9036.

- Margaritopoulos, J. T., Kasprovicz, L., Malloch, G. L. and Fenton, B. 2009. Tracking the global dispersal of a cosmopolitan insect pest, the peach potato aphid. – *BMC Ecol.* 9: 13.
- Martel, S. I., Ossa, C. G., Simon, J. C., Figueroa, C. C. and Bozinovic, F. 2020. Latitudinal trend in the reproductive mode of the pea aphid *Acyrtosiphon pisum* invading a wide climatic range. – *Ecol. Evol.* 10: 8289–8298.
- Martin, M. 2011. Cutadapt removes adapter sequences from high-throughput sequencing reads. – *EMBnet J.* 17: 10–12.
- Mathers, T. C. et al. 2017. Rapid transcriptional plasticity of duplicated gene clusters enables a clonally reproducing aphid to colonise diverse plant species. – *Genome Biol.* 18: 27.
- Medina, R. F., Armstrong, S. J. and Harrison, K. 2017. Genetic population structure of sugarcane aphid, *Melanaphis sacchari*, in sorghum, sugarcane, and Johnsongrass in the continental USA. – *Entomol. Exp. Appl.* 162: 358–365.
- Mizrahi-Man, O., Davenport, E. R. and Gilad, Y. 2013. Taxonomic classification of bacterial 16S rRNA genes using short sequencing reads: evaluation of effective study designs. – *PLoS One* 8: e53608.
- Montllor, C. B., Maxmen, A. and Purcell, A. H. 2002. Facultative bacterial endosymbionts benefit pea aphids *Acyrtosiphon pisum* under heat stress. – *Ecol. Entomol.* 27: 189–195.
- Nibouche, S., Costet, L., Medina, R. F., Holt, J. R., Sadeyen, J., Zoogones, A. S., Brown, P. and Blackman, R. L. 2021. Morphometric and molecular discrimination of the sugarcane aphid, *Melanaphis sacchari*, (Zehntner, 1897) and the sorghum aphid *Melanaphis sorghi* (Theobald, 1904). – *PLoS One* 16: e0241881.
- Nibouche, S., Fartek, B., Mississippi, S., Delatte, H., Reynaud, B. and Costet, L. 2014. Low genetic diversity in *Melanaphis sacchari* aphid populations at the worldwide scale. – *PLoS One* 9: e106067.
- Nibouche, S., Mississippi, S., Fartek, B., Delatte, H., Reynaud, B. and Costet, L. 2015. Host plant specialization in the sugarcane aphid *Melanaphis sacchari*. – *PLoS One* 10: e0143704.
- Nikolakakis, N. N., Margaritopoulos, J. T. and Tsitsipis, J. A. 2003. Performance of *Myzus persicae* (Hemiptera: Aphididae) clones on different host-plants and their host preference. – *Bull. Entomol. Res.* 93: 235–242.
- Nougé, O., Gallet, R., Chevin, L. M. and Lenormand, T. 2015. Niche limits of symbiotic gut microbiota constrain the salinity tolerance of brine shrimp. – *Am. Nat.* 186: 390–403.
- Oliver, K. M., Degnan, P. H., Burke, G. R. and Moran, N. A. 2010. Facultative symbionts in aphids and the horizontal transfer of ecologically important traits. – *Annu. Rev. Entomol.* 55: 247–266.
- Pagano, A., Lesbarrères, D., O'Hara, R., Crivelli, A., Veith, M., Lode, T. and Schmeller, D. S. 2008. Geographical and ecological distributions of frog hemiclones suggest occurrence of both 'General-Purpose Genotype' and 'Frozen Niche Variation' clones. – *J. Zool. Syst. Evol. Res.* 46: 162–168.
- Pantel, J. H., Juenger, T. E. and Leibold, M. A. 2011. Environmental gradients structure *Daphnia pulex pulicaria* clonal distribution. – *J. Evol. Biol.* 24: 723–732.
- Parker, E. D., Selander, R. K., Hudson, R. O. and Lester, L. J. 1977. Genetic diversity in colonizing parthenogenetic cockroaches. – *Evolution* 31: 836–842.
- Peccoud, J., Figueroa, C. C., Silva, A. X., Ramirez, C. C., Mieuze, L., Bonhomme, J., Stoeckel, S., Plantegenest, M. and Simon, J. C. 2008. Host range expansion of an introduced insect pest through multiple colonizations of specialized clones. – *Mol. Ecol.* 17: 4608–4618.
- Peterson, A. T., Soberón, J., Pearson, R. G., Anderson, R. P., Martinez-Meyer, E., Nakamura, M. and Araújo, M. B. 2011. Ecological niches and geographic distributions (MPB-49). – Princeton Univ. Press.
- Piffaretti, J., Vanlerberghe-Masutti, F., Tayeh, A., Clamens, A.-L., D'Acier, A. C. and Jouselin, E. 2012. Molecular phylogeny reveals the existence of two sibling species in the aphid pest *Brachycaudus helichrysi* (Hemiptera: Aphididae). – *Zool. Scr.* 41: 266–280.
- Piffaretti, J., Clamens, A. L., Vanlerberghe-masutti, F., Gupta, R. K., Call, E., Halbert, S. and Jouselin, E. 2013a. Regular or covert sex defines two lineages and worldwide superclones within the leaf-curl plum aphid (*Brachycaudus helichrysi*, Kaltentbach). – *Mol. Ecol.* 22: 3916–3932.
- Piffaretti, J., Rossi, J.-P., Vanlerberghe-Masutti, F., Genson, G., D'acier, A. C. and Jouselin, E. 2013b. Molecular identification and ecological characteristics of two cryptic lineages within a cosmopolitan aphid pest, *Brachycaudus helichrysi* (Hemiptera: Aphididae). – *Appl. Entomol. Zool.* 48: 155–164.
- Pluess, A. R. and Stöcklin, J. 2005. The importance of population origin and environment on clonal and sexual reproduction in the alpine plant *Geum reptans*. – *Funct. Ecol.* 19: 228–237.
- Popkin, M., Piffaretti, J., Clamens, A.-L., Qiao, G.-X., Chen, J., Vitalis, R., Vanlerberghe-Masutti, F., Gupta, R. K., Lamaari, M., Langella, O., Coeur d'acier, A. and Jouselin, E. 2017. Large-scale phylogeographic study of the cosmopolitan aphid pest *Brachycaudus helichrysi* reveals host plant associated lineages that evolved in allopatry. – *Biol. J. Linn. Soc.* 120: 102–114.
- Rognes, T., Flouri, T., Nichols, B., Quince, C. and Mahé, F. 2016. VSEARCH: a versatile open source tool for metagenomics. – *PeerJ* 4: e2584.
- Rothman, J. A., Leger, L., Graystock, P., Russell, K. and McFrederick, Q. S. 2019. The bumble bee microbiome increases survival of bees exposed to selenate toxicity. – *Environ. Microbiol.* 21: 3417–3429.
- Russell, J. A. and Moran, N. A. 2006. Costs and benefits of symbiont infection in aphids: variation among symbionts and across temperatures. – *Proc. R. Soc. B* 273: 603–610.
- Schoener, T. W. 1968. Sizes of feeding territories among birds. – *Ecology* 49: 123–141.
- Schön, I., Butlin, R. K., Griffiths, H. I. and Martens, K. 1998. Slow molecular evolution in an ancient asexual ostracod. – *Proc. R. Soc. B* 265: 235–242.
- Schön, I., Martens, K. and van Dijk, P. (eds). 2009. Lost sex. The evolutionary biology of parthenogenesis. – Springer.
- Van Doninck, K., Schön, I., De Bruyn, L. and Martens, K. 2002. A general purpose genotype in an ancient asexual. – *Oecologia* 132: 205–212.
- Van Doninck, K., Schön, I., Maes, F., De Bruyn, L. and Martens, K. 2003. Ecological strategies in the ancient asexual animal group Darwinulidae (Crustacea, Ostracoda). – *Freshwater Biol.* 48: 1285–1294.
- Vandel, A. 1940. La parthénogénèse géographique. IV. Polyploidie et distribution géographique. – *Bull. Biol. Fr. Belg.* 74: 94–100.
- Vandel, A. P. M. 1928. La parthéogénèse géographique: contribution à l'étude biologique et cytologique de la parthéogénèse naturelle. – Laboratoire d'Évolution des êtres organisés.
- Vorburger, C. 2014. The evolutionary ecology of symbiont-conferred resistance to parasitoids in aphids. – *Insect Sci.* 21: 251–264.
- Vorburger, C., Lancaster, M. and Sunnucks, P. 2003a. Environmentally related patterns of reproductive modes in the aphid *Myzus persicae* and the predominance of two 'superclones' in Victoria, Australia. – *Mol. Ecol.* 12: 3493–3504.
- Vorburger, C., Sunnucks, P. and Ward, S. A. 2003b. Explaining the coexistence of asexuals with their sexual progenitors: no evi-



- dence for general-purpose genotypes in obligate parthenogens of the peach-potato aphid, *Myzus persicae*. – *Ecol. Lett.* 6: 1091–1098.
- Vrijenhoek, R. C. 1979. Factors affecting clonal diversity and coexistence. – *Am. Zool.* 19: 787–797.
- Vrijenhoek, R. C. 1984. Ecological differentiation among clones: the frozen niche variation model. – In: *Population biology and evolution*. Springer, pp. 217–231.
- Vrijenhoek, R. C. and Parker, E. D. 2009. Geographical parthenogenesis: general purpose genotypes and frozen niche variation. – In: Schön, I., Martens, K. and Dijk, P. (eds), *Lost sex. The evolutionary biology of parthenogenesis*. Springer, pp. 99–131.
- Zhang, B., Leonard, S. P., Li, Y. and Moran, N. A. 2019. Obligate bacterial endosymbionts limit thermal tolerance of insect host species. – *Proc. Natl Acad. Sci. USA* 116: 24712–24718.