

Genetic diversity of the predatory mite Amblyseius swirskii Athias-Henriot (Acari: Phytoseiidae) with an overview of its distribution and implications for biological control

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1 Submitted to Biological Control 2 3 Genetic diversity of the predatory mite Amblyseius swirskii Athias-Henriot (Acari: 4 Phytoseiidae) with an overview of its distribution and implications for biological control 5 6 7 Tixier M.-S. *(1), Douin M. (1), Lopes I. (1), Migeon A. (2), Fossoud A. (3), Navajas M. (2) 8 9 (1) UMR CBGP, Montpellier SupAgro, INRA, CIRAD, IRD, Univ. Montpellier, Montpellier, 10 France. (2) CBGP, INRA, CIRAD, IRD, Montpellier SupAgro, Univ Montpellier, Montpellier, France. 11 12 (3) CBGP, IRD, INRA, CIRAD, Montpellier SupAgro, Univ Montpellier, Montpellier, France. E-mails: marie-stephane.tixier@supagro.fr, alain.migeon@inrae.fr, martial.douin@supagro.fr, 13 14 amandine.fossoud@ird.fr, maria.navajas@inrae.fr, ivinholoppes@gmail.com 15 * corresponding author 16 17 18 19

Abstract

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Amblyseius swirskii is a predatory mite of the family Phytoseiidae that is widely used in biological control of small insect and mite pests. A population from Israel was the source of material now commercially marketed by several biocontrol companies. The present study aimed to characterize the genetic variability of A. swirskii using 12S rRNA, CytB and COI mtDNA sequences, and explore its geographical distribution based on a compilation of known and newly-reported occurrences, including populations from several countries where this species naturally occurs. Amblyseius swirskii is reported from 22 countries, primarily in the eastern Mediterranean basin and Africa. The species has been reported on 48 plant families, with the highest number of observations on Rosaceae, Rutaceae and Solanaceae, mostly on crops, but also on uncultivated plants. The genetic diversity of A. swirskii was very low in all populations except the one from Cape Verde; all other studied populations were not differentiated from the commercial ones. The results suggest that commercialized and natural populations now co-occur widely, even in natural environments. The Cape Verde population seems to be a distinct natural population with relatively high intra-population variation, even among specimens collected in a single locality and on a single plant species. Further analyses would be required to determine how much the observed genetic differentiation results in different biological features, but the diversity present in the natural Cape Verde populations of A. swirskii may provide a source of novel traits with potential to improve the performance of this natural enemy.

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Key-words: biodiversity, geographic distribution, population differentiation

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Introduction

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2 Mites of the family Phytoseiidae are predators and some species among the 2,521 described 3 are currently used for biological control issues (Gerson et al., 2003; Demite et al., 2020; Van 4 Lenteren, 2012; Van Lenteren et al., 2017). Some of these species are commercialised and 5 mass-released on crops for augmentative biological control strategies (Knapp et al., 2018). 6 One of the most recently commercialised species of Phytoseiidae is Amblyseius swirskii 7 Athias-Henriot, marketed since 2005 and now sold in more than 50 countries (Calvo et al., 8 2015). This species is used to control mite pests (i.e. Tetranychus urticae (Koch) and 9 Polyphagotarsonemus latus Banks) and small insects (thrips and whiteflies). Recent reviews 10 provide a synthesis of the preys it can feed on, and give the reasons for its great commercial 11 success (Buitenhuis et al., 2015; Calvo et al., 2015). Amblyseius swirskii is a generalist 12 predator, like most of Phytoseiidae mites, able to develop on various preys (including other 13 Phytoseiidae species) and also pollen (McMurtry et al., 2013; Buitenhuis et al., 2015). 14 Because of its commercial interest, the biology of this species has been extensively studied 15 and is relatively well known. Differences in biological features have been observed, 16 especially between wild and commercial populations (Cerqueira Cavalcante et al., 2015). 17 Recently, Paspati et al. (2019), using a low number of microsatellites markers, detected a 18 lower genetic diversity in commercial vs wild populations. While the factors determining wild 19 population structure are not identified, plants with high trichome densities are assumed to 20 limit population development, affecting genetic diversity. Understanding the structuration of 21 the populations and possible associated biological features is essential for improving efficacy 22 of biological control practices. Commercial populations are often mass-reared for long 23 periods. Bottlenecks and genetic drift are expected, which can lower genetic diversity and 24 thus the adaptation potential, when specimens are released in very contrasted environments 25 (Roderick and Navajas, 2003). Recent studies exploring possible relationships between 26 genetic differentiation and biological features, show slight differences in populations of 27 Typhlodromus (Anthoseius) recki Wainstein and Phytoseiulus longipes Evans (using 12S 28 rRNA sequences) potentially associated with feeding habits (Tixier et al., 2010a; Tixier et al., 29 2021). Likewise, differences in amino acid sequences of the mitochondrial Cytb sequence in 30 several species of Phytoseiidae mites seem to be associated with adaptation to climatic 31 conditions (Queiroz et al., 2021; Tixier et al., 2021). 32 This study investigates genetic diversity in different populations of A. swirskii collected in 33 several locations in Israel and Africa, including La Reunion and Cape Verde islands. The

hypothesis tested is that genetic diversity exists between / within these localities, but as we

- 1 have no information on the biological features of these populations, no relationship between
- 2 genetic variation and biological parameters will be herein tested. In addition, this study
- 3 compiles data on the known world distribution of A. swirskii, including host plants and
- 4 climatic conditions, as a baseline for further search of natural populations potentially
- 5 interesting for biological control.

Material & methods

- 8 Amblyseius swirskii distribution. Information on the geographic distribution and host plants
- 9 was retrieved from 46 publications (from 1962 to 2020) recording A. swirskii occurrences
- 10 (dataset available in the supplementary file 1.). An occurrence is considered as a report on a
- plant species per publication. This compilation also includes the occurrences of the synonyms
- of A. swirskii (Amblyseius capsicum (Basha, Yousef, Ibrahim & Mostafa), Amblyseius enab
- 13 El-Badry, Amblyseius rykei Pritchard & Baker). In this study, we followed the Angiosperm
- 14 Phylogeny Group III's nomenclature (2009) for family, genus and species names.

15 Genetic analyses

- 16 Commercial populations sold by different biological control companies and wild populations
- 17 collected in Benin, Cape Verde, Egypt, Israel and Reunion Island were studied. The
- characteristics of these populations are presented in the Table 1, together with DNA sequence
- accession numbers in the Genbank database.
- Three mitochondrial molecular markers were considered: 12S rRNA, Cytb and COI mtDNA.
- 21 These markers were chosen because previous studies proved their variability at intraspecific
- level in Phytoseiidae species (Dos Santos and Tixier, 2017; Tixier et al., 2010a, 2021;
- 23 Queiroz et al., 2021). DNA extractions were carried out on single female specimens,
- 24 following the protocol accurately described in Kanouh et al. (2010) and using the Qiagen
- 25 modified process. After DNA extraction, mite carcasses were recovered and mounted on
- slides as described by Tixier et al. (2010b). The primers and the PCR conditions were as
- described in Tixier et al. (2012). The sequences were aligned and analysed using the MEGA
- 28 X software (Kumar et al. 2018). The alignments are available in the supplementary file 2. The
- sequences obtained were compared to those included in the GenBank database to identify
- 30 possible contaminations. Genetic distances (using the Kimura 2 parameter) were calculated
- 31 for comparing DNA sequences. Maximum likelihood trees were constructed; the best-fit-
- 32 substitution model (TrN+I for the 12S rRNA marker, HKY+I for COI mtDNA marker,
- 33 HKY+I for the Cytb mtDNA marker) was determined by Modeltest 3.07 (Posada and
- Crandall, 1998) in PAUP* v.4.0b.10 (Swofford 2002) through hierarchical likelihood-ratio

- 1 tests. The out-group species used was Amblyseius andersoni Chant, a sister species of A.
- 2 swirskii (Genbank accession numbers for COI mtDNA: KU318176, for Cytb mtDNA
- 3 KU318207, for 12S rRNA: HQ404858). In addition, a concatenated tree was constructed
- 4 (supplementary file 3) with the specimens, for which DNA sequences were available for the
- 5 three markers.

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Results and discussion

- 9 Amblyseius swirskii distribution. 257 occurrences were retrieved from the literature
- including the three synonym species (226 for A. swirskii, 6 for A. enab, 1 for A. capsicum and
- 24 for A. rykei) (Table 2). Amblyseius swirskii is reported in 22 countries, A. enab and A.
- 12 capsicum in Egypt only and A. rykei in seven African countries (Ethiopian region). Before
- 13 2005 (first commercialisation of A. swirskii), this species (A. swirskii and its synonyms) was
- 14 reported in 15 countries (Egypt, Cape Verde, Italy, Turkey, Israel, Azerbaijan, Georgia,
- 15 Yemen, Kenya, Benin, Ghana, Nigeria, Zimbabwe, Democratic Republic of Congo, Cuba),
- both in crops (33% of the reports 37 cultivated species belonging to 15 plant families,
- among which eight species were Citrus and six were Solanum) and uncultivated plants (67%
- of the reports). Because of the current distribution of A. rykei (only reported in Africa) and
- difficulties to identify morphologically close species, the report of A. rykei in Cuba (Martinez
- et al., 2004) on Musa paradisiaca in 1978 is quite doubtful and a misidentification can be
- 21 suspected.
- 22 On the 218 occurrences (for A. swirskii and its three synonyms) reported before 2005, 85%
- are recorded from only three countries geographically close: Israel (160 reports), Gaza strip (2
- reports) and Egypt (24 reports). The second region where A. swirskii is widely spread is West
- 25 Africa. All the reports in this latter area, before 2005, correspond to the species A. rikey
- 26 (except in Cape Verde) (Table 2). This latter species was synonymised with A. swirskii
- 27 (Zannnou et al., 2007; Zannou and Hanna, 2011), after observing the type specimen of A.
- 28 rikey and conducting crossbreeding experiments, using specimens collected in Benin
- 29 (Atcherigbe) in 2008 and Israël. The distribution of A. swirskii is very puzzling, as there is a
- 30 great geographical gap between the Middle-East (A. swirskii main occurrences) and African
- 31 locations (A. rykei main occurrences), as this species was never reported in Maghreb
- 32 (Morocco, Tunisia, Algeria) despite intensive surveys in these countries (Kreiter et al., 2002,
- 33 2006; Sahraoui et al., 2012; Tixier et al., 2003, 2016). Even if synonymy was affirmed
- 34 (Zannnou et al., 2007; Zannou and Hanna, 2011), the differentiated distribution of these two

1 species can question this statement. Two hypotheses can be put forward (i) A. rikey is not a 2 synonym of A. swirskii and the African specimens considered by Zannou and Hanna (2011) 3 for crossbreedings were actually issued from commercial releases of A. swirskii, or (ii) A. 4 rikey is a synonym of A. swirskii and gaps in the geographical distribution are explained by 5 particular climatic conditions. As we have not further evidences, we will consider here that 6 these two species are synonyms. 7 Amblyseius swirskii is reported on 132 plant species (122 before 2005 and 19 after 2005), belonging to 97 genera and 48 families. The number of reports per plant family varies from 1 8 9 to 34. The plant families where A. swirskii was collected most often are Rosaceae (34 reports), Rutaceae (30 reports), Solanaceae (19 reports), Leguminosae (12 reports), 10 11 Compositae (11 reports) and Malvaceae (10 reports) (Table 3). These reports mainly 12 correspond to cultivated plants but some wild plants are also represented, showing a great 13 ability of the species to occur on a diversity of plants belonging to a wide range of families. 14 Publications do not always report the presence of prey in association with A. swirskii, 15 preventing any link to be done between the presence of A. swirskii and its prey. However, as a 16 generalist predator this species can feed on other food sources (e.g. pollen thrips, whiteflies) 17 and the presence of prey is certainly not the main driver of its presence (McMurtry et al., 18 2013). Besides the number of reports, an important aspect to take into account is the number 19 of specimens collected on each plant species; unfortunately this information is not always 20 provided in the publications, and when provided they are not comparable because collection 21 methods differ between reports. Interestingly, the plant species where A. swirskii and A. rykei 22 were observed are not very different. Even if A. swirskii is clearly reported on more plant 23 families (42) than A. rykei (14), both are reported on eight common plant families, which is 24 about 60% of the A. rykei plant range (8 out of 14). Six plant families are only "colonised" by 25 A. rikey (Actinidiaceae, Musaceae, Acanthaceae, Araceae, Cannabaceae, Proteaceae) (Table 26 3), but this can be due to sampling bias. The host plant does not appear as a main factor 27 explaining the differentiation between African populations (A. rikey) and Middle-East 28 populations of A. swirskii. 29

Genetic analyses. The phylogenetic trees obtained with 12S rRNA, Cytb and COI mt DNA sequences congruently show the same population differentiation (Figures 3a-c), with samples gathered in two main clades. One clade contains all the specimens considered, except specimens collected in Cape Verde, while all specimens from Cape Verde are grouped apart, excepting one (collected in this country at the same locality and on the same plant as the

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- 1 others).
- 2 Genetic distances among the 34, 54 and 40 specimens of A. swirskii here considered, range
- 3 between 0 and 2.4%, 0 and 8.4 % and 0 and 4.2% for the 12S rRNA, Cytb and COI markers,
- 4 respectively (Table 4a-c). For all sequences, the highest mean genetic distances were
- 5 observed between specimens from Cape Verde and the others (Table 4a-c). When regarding
- 6 the mean genetic distances among the populations, excluding Cape Verde, they were all very
- 7 low, ranging from 0 to 1% for 12S rRNA, from 0.1% to 1% for Cytb mtDNA and from 0.1%
- 8 to 0.3% for the COI mtDNA. One Cape Verde specimen appears clearly apart and differs
- 9 from the other Cape Verde specimens by a distance of 1.7 % for 12S rRNA, 8.4% for Cytb
- 10 mtDNA and 4.2% for the COI mtDNA. When excluding this specimen, intra-population
- variation in Cape Verde is null and distances to the other populations range from 1.3 to 2 %
- 12 for 12S rRNA, from 2 to 2.6% for the Cytb mtDNA and from 2.4 to 2.6% for the COI
- 13 mtDNA. The genetic distances among the specimens herein considered, even if quite high,
- 14 especially considering the Cape Verde specimens, clearly correspond to intraspecific
- variations. The highest intraspecific distances found in literature for 12SrRNA, Cytb mtDNA
- and COI mtDNA are 7.8% (for Amblyseius largoensis (Muma) in Barbosa-Lima et al. (2018),
- 17 23% (for Phytoseius finitimus Ribaga in Tixier et al. (2017)) and 10.5% (for Neoseiulus
- californicus (McGregor) in Okassa et al. (2011)), respectively. We can thus conclude that all
- 19 the specimens here studied belong to the species Amblyseius swirskii. Even if the genetic
- distances within the Cape Verde population are much higher than those within the other
- 21 populations herein considered, they are relatively small comparing to the intraspecific
- variations observed for other Phytoseiidae species (e.g. Okassa et al., 2011; Tixier et al.,
- 23 2017).
- 24 Very low diversity was found between Egyptian, Israeli, Reunion Island, Benin and
- commercial populations. Commercial populations, whatever the selling company, show very
- low diversity, probably because they are all issued from the same original strain. The Koppert
- 27 commercial population was issued from Israel, which might explain its proximity with the
- 28 Israeli specimens examined in this study.
- 29 The Reunion specimens are also very similar to commercial strains, which supports
- 30 conclusions by Kreiter et al. (2016) using morphological and 12S rRNA marker, on a
- 31 commercial mass-released origin. No differentiation was detected between the two Benin
- 32 populations, despite their assumed different origin (Israel: reared since 2007 in lab conditions
- and Benin: wild population collected in 2016 and then reared in the lab). Several hypotheses
- 34 can be put forward to explain this absence of differentiation and the high similarity with

1 commercial populations: (i) a contamination in rearing units and an overpass between the 2 commercial strain and the wild specimens, (ii) the wild population (collected in Benin on 3 Solanum macrocarpon) is not a wild population and is issued from a released commercial 4 strain, or a non-documented intentional or non-intentional introduction, as often occurred 5 during the 1960-1980 period, or (iii) the wild population is really wild but not differentiated 6 from the others despite the geographical distance where specimens were collected. The 7 Egyptian population is also not differentiated from the commercial strain. This situation might 8 result from a mix of commercialised specimens that spread on citrus crops, and reproduced 9 with the "rare" natural specimens with perhaps less fitness parameters. Globally, the diversity 10 between the populations considered (except in Cape Verde) is low for the three markers 11 considered. 12 A higher diversity in the wild populations than in the commercial strains and a differentiation 13 between them was expected, as showed by Paspati et al. (2019) by using six microsatellite 14 markers to compare eight populations collected in Israel (on five crops) to a Koppert 15 commercial population. It is difficult to compare the results herein obtained and those of these 16 authors, as the populations studied (only Israelian populations in Paspati et al. (2019)), the 17 number of specimens (higher and pooled in Paspati et al. (2019)) and the molecular markers 18 used were different. Two facts could account for the absence of differentiation herein 19 observed between all populations (except Cape Verde): i) a high gene flow between remote 20 populations (although it is not consistent with the results obtained by Paspati et al. (2019) 21 where low Fst were observed between populations collected in a same country), or ii) the higher polymorphism of microsatellite markers compared to mitochondrial sequences 22 23 (maternally inherited) (Avise, 1994; Zhang and Hweitt, 2003). Additional mitochondrial 24 DNA sequencing on the specimens / populations considered by Paspati et al. (2019) together 25 with microsatellite analysis carried on the word distributed populations herein considered, 26 would be highly informative. However, the most consistent hypothesis would be that most of 27 populations considered, even if collected in wild conditions, were issued from commercial 28 introductions. 29 A relevant genetic variability at intra-population level was only detected among specimens of 30 Cape Verde. In island conditions, a funder effect could be expected (e.g. Frankham, 1997) 31 reflected by a reduced genetic diversity in island populations compared to mainland, which 32 did not emerged from this study. Two hypotheses can be putted forward to explain these 33 results: (i) a funder effect exists as the genetic diversity within the Cape Verde population is 34 low compared to genetic diversity observed for Phytoseiidae wild populations of other species

(e.g. Okassa et al., 2011; Tixier et al., 2017), but this funder effect was not detected because all mainland populations herein tested are issued from commercial introductions, or (ii) a funder effect has existed but was compensated by recent and/or recurrent exchanges between Cape Verde and mainland populations, especially from Africa (due to trade and important commercial exchanges existing between the two regions). The specimens collected in Cape Verde are clearly not from a commercial population; samples were collected from an uncultivated plant in a remote valley in the San Antao Island. In a survey carried out in other islands of the Cape Verde archipelago (data unpublished), A. swirskii was found in the Island of Santiago on bean co-planted with maize (only one specimen retrieved, which could not be molecular typed). Ueckermann (1992) also reported this species from Cape Verde in several localities (in Paul-San Antao Island, in Sao Jorge dos Orgaos and Santa Cruz - Santiago Island). Seen together, data tend to suggest that A. swirskii has settled in this archipelago although the origin of this colonisation remains to be elucidated. Several hypotheses can be proposed as (i) an introduction from Africa or (ii) an introduction from Middle East. The basal position of the Cape Verde population of the phylogenetic trees would suggest that the other populations herein considered are issued from Africa. This hypothesis would be in accordance with the presence of this species (especially under the name A. rykei) in West Africa before 2005. However, the use of additional markers especially nuclear ones is needed to further explore this hypothesis, together the study of additional Israeli samples and natural / wild specimens from Africa. Additionally, it would be interesting to further explore biological traits of interest in A. swirskii from Cape Verde, as previous studies suggested some link between genetic differences and biological features, e.g. climate adaptation (for COI and Cytb mtDNA) and prey adaptation (for 12S rRNA) (Tixier et al., 2010a, 2021; Queiroz et al., 2021). Even if these markers are usually considered neutral, some studies have shown that mutations can be associated to abiotic factors (pesticide resistance in Tetranychus urticae (Koch) (Van Nieuwenhuyse et al., 2009; Fotoukkiaii et al., 2020), temperature adaptation in anchovies and Lottia in COI mtDNA sequences (Dong et al., 2009; Silva et al. 2014)). Likewise, intrapopulation differentiation observed in Cape Verde in mites collected in a single location and on the same plant species tend also to suggest significant A. swirskii diversity in the Sao Antao island; it would be thus interesting to enlarge investigation of A. swirskii in Cape Verde and Africa for capturing genetic diversity in A. swisrkii, which is in turn a keystone for the management of commercial biocontrol agents.

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Conclusion

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- 2 Genetic diversity in A. swirskii is low, despite the wide sampling here considered where all
- 3 specimens, except the ones collected in Cape Verde, were not clearly differentiated from the
- 4 commercial ones. Two non-exclusive hypotheses could explain these results: an incursion in
- 5 natural environments by individuals originated from commercial strains and/or a low intra-
- 6 species diversity of A. swirskii.
- 7 Genetic diversity captured in Cape Verde, could be explained by the introduction of the mite
- 8 in this archipelago long time ago; while firstly recorded in 1984, 1985 and 1987 by
- 9 Ueckermann (1992). Genetic distances between those mites and all the other populations
- 10 considered were however low in comparison with intraspecific genetic distances observed
- between wild populations of Typhlodromus (Typhlodromus) pyri Scheuten, Typhlodromus
- 12 (Typhlodromus) phialatus Athias-Henriot, N. californicus or P. finitimus (Okassa et al., 2011;
- 13 Tixier et al., 2012, 2017). The present study contributes to estimate the biodiversity of A.
- swirskii and while providing a partial picture of the diversity of the species, is as far as we
- know the only available. The obtained results open perspectives for investigating furtherly
- 16 functional traits of the mite associated to genetic differences, in particular climate and prey
- adaptation, as two of relevant traits to be explored to improve the efficacity of species used
- 18 for biocontrol purposes.

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References

- Avise, J.C., 1994. Molecular markers. Natural history and evolution. New York: Chapman
- 28 & Hall.
- 29 Barbosa Lima, D., Rezende-Puker, D., Santos de Mendonça, R., Tixier, M.-S., Guedes
- Correia Gondim Junior, M., Wagner da Silva Melo, J., Chiaradia Oliveira, D., Navia, D.,
- 31 2018. Molecular and morphological characterization of the predatory mite *Amblyseius*
- 32 largoensis (Acari: Phytoseiidae). Surprising similarity between an Asian and American
- 33 populations. Exp. Appl. Acarol. 76, 287–310.

- 1 Buitenhuis, R., Murphy, G., Shipp, L., Scott-Dupree, C., 2015. Amblyseius swirskii in
- greenhouse production systems: a floricultural perspective. Exp. Appl. Acarol. 65(4), 451-
- 3 464. doi:10.1007/s10493-014-9869-9
- 4 Calvo, F.J., Knapp, M., van Houten, Y.M., Hoogerbrugge, H., Belda, J.E., 2015. Amblyseius
- 5 *swirskii*: What made this predatory mite such a successful biocontrol agent? Exp. Appl.
- 6 Acarol. 65, 419–433. https://doi.org/10.1007/s10493-014-9873-0
- 7 Cerqueira Cavalcante, A.C., Borges, L.R., Lourençao, A.L., Moraes, G.J., 2015. Potential of
- 8 two populations of Amblyseius swirskii (Acari: Phytoseiidae) for the control of Bemisia
- 9 *tabaci* biotype B (Hemiptera: Aleyrodidae) in Brazil. Exp. Appl. Acarol. 67(4), 523-33.
- doi: 10.1007/s10493-015-9964-6
- Demite, P.R., Moraes, G.J. de, McMurtry, J.A., Denmark, H.A., Castilho, R.C., 2020.
- Phytoseiidae Database. Available from: www.lea.esalq.usp.br/phytoseiidae (accessed
- 13 15/II/2020)
- 14 Dong, Y., Somero, G.N., 2009. Temperature adaptation of cytosolic malate
- dehydrogenases of limpets (genus Lottia): differences in stability and function due to
- minor changes in sequence correlate with biogeographic and vertical distributions. J.
- 17 Exp. Biol. 212, 169-177.
- 18 Dos Santos, V., Tixier, M.-S., 2017. Molecular markers for analysing phylogenetic
- relationships within the mite family Phytoseiidae (Acari: Mesostigmata). Cladistics 28(5),
- 20 1-16.
- Fotoukkiaii, S.M., Tan, Z., Xue, W., Wybouw, N., Van Leeuwen, T., 2020. Identification and
- 22 characterization of new mutations in mitochondrial cytochrome b that confer resistance to
- bifenazate and acequinocyl in the spider mite *Tetranychus urticae*. Pest Manag. Sci. 73(3),
- 24 1154-1163.
- 25 Frankham R. 1997. Do island populations have less genetic variation than mainland
- populations? Heredity 78, 311-327.
- Gerson, U., Smiley, R. L., Ochoa, T., 2003. Mites (Acari) for Pest Control. Oxford, UK:
- 28 Blackwell Science.
- 29 Kanouh, M., Tixier, M.-S., Okassa, M., Kreiter, S., 2010. Phylogenetic and biogeographic
- analysis of the genus *Phytoseiulus* (Acari: Phytoseiidae). Zool. Scr. 39, 450-461.
- 31 doi:10.1111/j.1463-6409.2010.00439.x
- Knapp, M., Van Houten, Y., Van Baala, E., Groot, T., 2018. Use of predatory mites in
- commercial biocontrol: current status and future prospects. Acarologia 58(Suppl), 72-82; DOI
- 34 10.24349/acarologia/20184275

- 1 Kreiter, S., Auger, P., Lebdi Grissa, K., Tixier, M.-S., Chermiti, B., Dali, M., 2002. Plant
- 2 inhabiting mites (Acari: Prostigmata & Mesostigmata) of some Northern Tunisian
- 3 crops. Acarologia 42(4), 389-402.
- 4 Kreiter, S., Dos Santos Vicente, V., Tixier, M.-S., Fontaine, O., 2016. An unexpected
- 5 occurrence of Amblyseius swirskii Athias-Henriot in La Réunion Island (Acari:
- 6 Phytoseiidae). Acarologia 56(2), 175-181.
- 7 Kreiter, S., Tixier, M.-S., Auger, P., Cheval, B., Lebdi Grissa, K., 2006. Phytoseiid mites
- 8 (Acari: Mesostigmata) of Southern Tunisia. Acarologia 46(1-2), 5-13.
- 9 Kumar, S., Stecher, G., Li, M., Knyaz, C., Tamura, K., 2018. MEGA X: Molecular
- Evolutionary Genetics Analysis across computing platforms. Mol. Biol. Evol. 35, 1547-
- 11 1549.
- Martinez, A.Z., de la Torre, P.E., García, S.A., 2004. Principales ácaros detectados em la
- 13 Província de Villa Clara. Fitosanidad 8(1), 3–17.
- 14 McMurtry, J.A., Moraes, G.J. de, Sourasso, N.F., 2013. Revision of the life styles of
- phytoseiid mites (Acari: Phytoseiidae) and implications for biological control strategies.
- 16 Syst. Appl. Acarol. 18, 297-320.
- Okassa, M., Kreiter, S., Guichou, S., Tixier, M.-S., 2011. Molecular and morphological
- boundaries of the predator *Neoseiulus californicus* McGregor (Acari: Phytoseiidae).
- 19 Biol. J. Linn. Soc. 104, 393-406.
- Paspati, A., Ferguson, K.B., Verhulst, E.C., Urbaneja, A., Gonzalez-Cabrera, J., Pannebakker,
- B.A., 2019. Effect of mass rearing on the genetic diversity of the predatory mite
- 22 Amblyseius swirskii. Entomol. Experim. Appl. 167, 670–681.
- Posada D., Crandall K.A., 1998. Modeltest: testing the model of DNA substitution.
- 24 Bioinformatics 14, 817–818.
- Queiroz, M. C., Douin, M., Marques de Souza, S., Sato, E, Tixier, M.-S., 2021. Molecular
- variations of the Cytochrome b DNA and protein sequences in *Phytoseiulus macropilis*
- Banks (Acari: Phytoseiidae) and *P. persimilis* (Athias-Henriot) (Acari: Phytoseiidae)
- reflect population structuration. Exp. Appl. Acarol. 84(4), 687-701. doi: 10.1007/s10493-
- 29 021-00648-w.
- Roderick, G., Navajas M., 2003. Genes in new environments: Genetics and evolution in
- biological control. Nature reviews 4, 889-899.
- 32 Sahraoui, H., Lebdi Grissa, K., Kreiter, S., Douin, M., Tixier, M.-S., 2012. Phytoseiid mites
- 33 (Acari: Mesostigmata) of Tunisian Citrus orchards. Acarologia 52(4), 433-452.

- 1 Silva, G., Lima, F.P., Martel, P., Castilho, R., 2014. Thermal adaptation and clinal
- 2 mitochondrial DNA variation of European anchovy. Proc. R. Soc. series B (281), 1093.
- 3 http://dx.doi.org/10.1098/rspb.2014.1093
- 4 Swofford D.L., 2002. PAUP. Phylogenetic Analysis Using Parsimony and other methods.
- 5 Ver. 4.0b.10. Sinauer Associates, Inc.
- 6 The Angiosperm Phylogeny Group. 2009. An update of the Angiosperm Phylogeny Group
- 7 classification for the orders and families of flowering plants: APG III. Botan. J. Linn. Soc.
- 8 161, 105-121. doi:10.1111/j.1095-8339.2009.00996.x
- 9 Tixier, M.-S., Allam, L., Douin, S., Kreiter, S., 2016. Phytoseiidae (Acari: Mesostigmata) of
- Morocco: new records, descriptions of five new species, re-descriptions of two species and
- key for identification. Zootaxa 4067(5), 501-551.
- 12 Tixier, M.-S., Dos Santos, V., Douin, M., Duso, C., Kreiter, S., 2017. Great molecular
- variation within the species *Phytoseius finitimus* (Acari: Phytoseiidae): implications for
- diagnosis decision within the mite family Phytoseiidae. Acarologia 57(3), 493–515.
- 15 Tixier, M.-S., Ferrero, M., Okassa, M., Guichou, S., Kreiter, S., 2010a. On the specific
- identity of specimens of Phytoseiulus longipes Evans (Mesostigmata: Phytoseiidae)
- showing different feeding behaviours: morphological and molecular analyses. Bull.
- 18 Entomol. Res. 100(5), 569-579. doi:10.1017/S0007485309990617
- 19 Tixier, M.-S., Kreiter, S., Allam, L., Ouahbi, A., Hmimina, H., 2003. Phytoseiid and
- tetranychid mites (Acari: Mesostigmata) of some Moroccan crops. Acarologia 43(1),
- 21 87-97.
- Tixier, M.-S., Okassa, M., Liguori, M.L., Poinso, A., Salerno, B., Kreiter, S., 2010b. Voucher
- specimens for DNA sequences of Phytoseiid mites (Acari: Mesostigmata) Acarologia
- 24 50(4), 487-494.
- 25 Tixier, M.-S., Okassa M., Kreiter, S., 2012. An integrative morphological and molecular
- 26 diagnostics for *Typhlodromus pyri* (Acari: Phytoseiidae). Zool. Scr. 41, 68-78.
- 27 Tixier, M.-S., Perez, Martinez, S., Douin, M., 2021. Markers of life history traits: variation in
- morphology, molecular and amino acid sequences within *Typhlodromus* (*Anthoseius*)
- 29 recki Wainstein (Acari: Mesostigmata: Phytoseiidae). Biol. J. Linn. Soc. 132 (1), 53–73.
- 30 https://doi.org/10.1093/biolinnean/blaa103
- 31 Van Lenteren, J.C., 2012. The state of commercial augmentative biological control: plenty of
- natural enemies, but a frustrating lack of uptake. BioControl 57, 1–20. DOI
- 33 10.1007/s10526-011-9395-1

- 1 Van Lenteren, J.C., Bolckmans, K., Köhl, J., Ravensberg, W.J., Urbaneja, A., 2017.
- 2 Biological control using invertebrates and microorganisms: plenty of new opportunities.
- 3 BioControl 63, 39–59 (2018). https://doi.org/10.1007/s10526-017-9801-4
- 4 Van Nieuwenhuyse, P., Van Leeuwen, T., Khajehali, J., Vanholme, B., Tirry, L., 2009.
- Mutations in the mitochondrial cytochrome b of Tetranychus urticae Koch (Acari:
- 6 Tetranychidae) confer cross-resistance between bifenazate and acequinocyl. *Pest Manag*.
- 7 *Sci.* 65, 404–412.

- 8 Zhang, D.X., Hweitt, G.M., 2003. Nuclear DNA analyses in genetic studies of populations:
- 9 Practice, problems and prospects. Mol. Ecol. 12, 563–584.

Captions of figures

1 2

Figure 1. Current distribution of *Amblyseius swirskii*. The original name used for each record is indicated. Country distribution level reports the supposed status of the populations. Data compilated from the literature and records from this study.

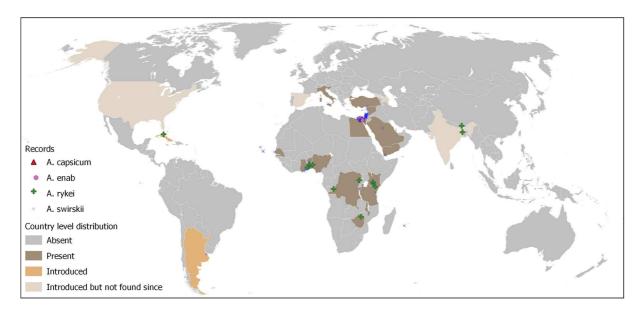
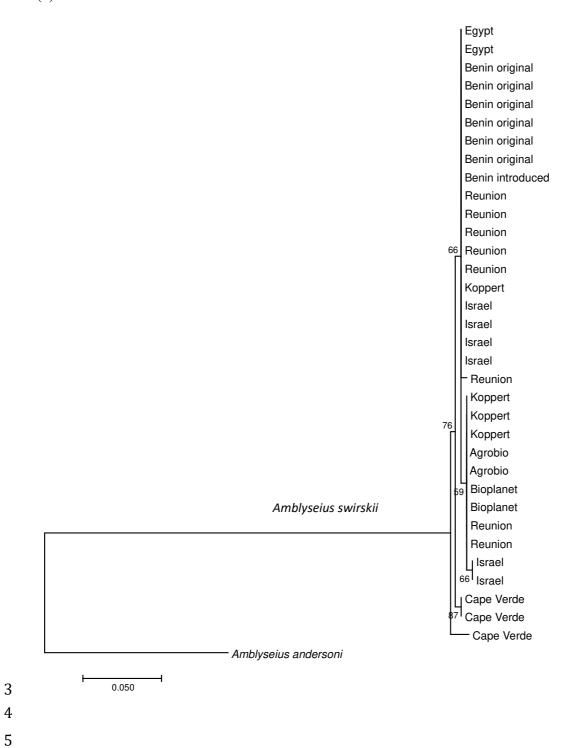


Figure 2. Maximum Likelihood phylogenetic trees including specimens of *A. swirskii* and *A. andersoni* (as an outgroup) obtained with (a) 12S rRNA, (b) COI mtDNA and (c) CytB mtDNA sequences.

1 Figure 2

2 (a) 12S rRNA

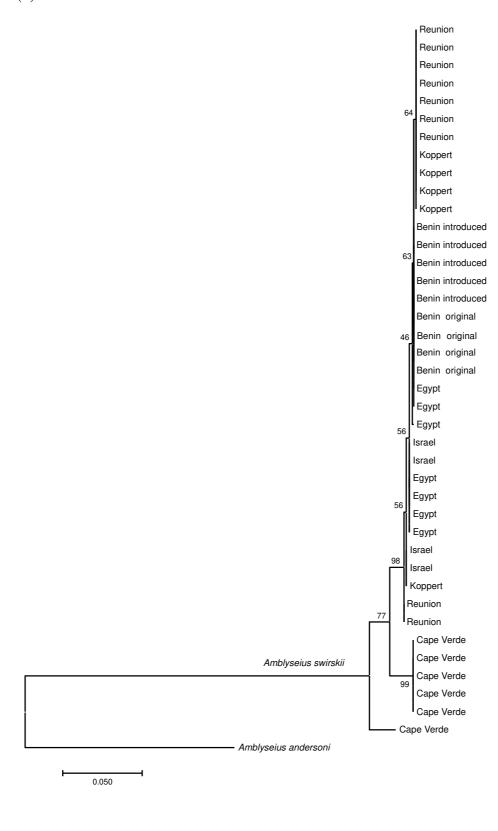


1 Figure 2

3 4

5

2 (b) COI mtDNA



1 Figure 2

2 (c) CytB mtDNA

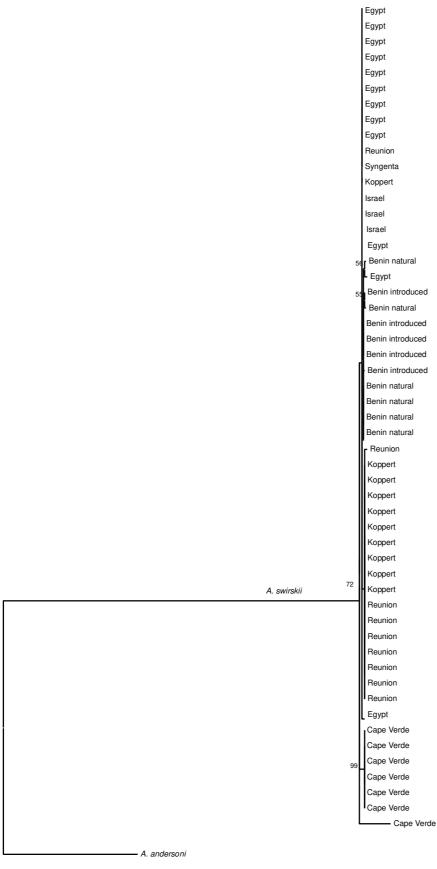


Table 1. Accession numbers for 12S rRNA, COI and CytB mitochondrial sequences deposited in Genbank and geographical locations and plants where *Amblyseius swirskii* were collected.

			Genbank accession	Genbank accession numbers CytB	Genbank accession numbers COI
ountry / company	Locality	Host plant	numbers 12S rRNA	mtDNA	mtDNA
Koppert	commercial strain from France	not known	MW404020, MW404021,	MT828779, MT828780, MT828781,	MT827885, MT827886, MT827887
			MW404022, MW404023	MT828782, MT828783, MT828797,	MT827888, MT827889
			(n=4)	MT828798, MT828799, MT828800,	(n=5)
				MT828801	
				(n=10)	
Agrobio	commercial strain	not known	MW404026, MW404027	-	
			(n=2)		-
BioPlanet	commercial strain	not known	MW404028, MW404029	-	
			(n=2)		-
Syngenta	commercial strain	rearings	-	MT828784	
				(n=1)	-
France Reunion	Montvert (55°32'19"S, 21°19'42"E)	Capsicum annuum	KX064698, KX064699,	MT828785, MT828786, MT828787,	MT827876, MT827877, MT827878
island		(Solanaceae)	KX064700, KX064701,	MT828788, MT828789, MT828790,	MT827879, MT827880, MT827881
			KX064702, KX064703,	MT828791, MT828792, MT828793	MT827882, MT827883, MT827884
			KX064697, KX064704	(n=9)	(n=9)
			(n=8)		
Israel	Acre (32°56'37.367"N 35°6' 8.139'E') and	Citrus sp. (Rutaceae)	MW404024, MW404025,	MT828794, MT828795, MT828796	MW074353, MW074354,
	Hula Valley (32°56'37.367"N 35°6' 8.139"E)		MW411334, MW411335,	(n=3)	MW074355, MW074356
			MW411336 , MW4113367		(n=4)
			(n=6)		
Benin	Idigny (7°28'19.7"N 2°41'01.8"E)	Solanum macrocarpon	MW404031, MW404032,	MT828808, MT828809, MT828810,	MT819959, MT819960, MT819961,
		(Solanaceae)	MW404033, MW404034,	MT828811, MT828812	MT819962
			MW404035, MW404036	(n=5)	(n=4)
			(n=6)		
	Brazilian population issued from Israel	Not known	MW404030	MT828807, MT828814, MT828815,	MT827915, MT827916, MT827917
			(n=1)	MT828816, MT828817	MT827918, MT827919
				(n=5)	(n=5)
Egypt	Al-Azizia, Sharqia Governorate (30°02'44.6"N	Citrus sp. (Rutaceae)	MW404037, MW404038	MT828819, MT828820, MT828821,	MT827899, MT827900, MT827901
	31°10'56.0"E)		(n=2)	MT828822, MT828823, MT828824,	MT827902, MT827903, MT827904
				MT828825, MT828826, MT828827,	(n=6)
				MT828828, MT828829, MT828830	, ,
				(n=12)	
Cape Verde	Ribeira da Torre (17°8'13"N, -25°3'58"E)	Ageratum conyzoides	MW404039, MW404040,	MT828802, MT828803, MT828804,	MT827894, MT827895, MT827896
•	, ,	(Asteraceae)	MW404041	MT828805, MT828806, MT828813,	MT827897, MT827898, MT828365
		· · · · · · · · · · · · · · · · · · ·	(=3)	MT828818	(n=6)
			, -,	(n=7)	, -/

- Table 2. Number of reports per country of Amblyseius swirskii and Amblyseius rikey before
- and after 2005 (first known commercialisation of A. swirskii).

	Number of repor	ts before 2005	Number of reports after 2005			
	A. swirskii	A. rikey	A. swirskii	A. rikey		
Argentina			1			
Azerbaijan	1					
Benin		2	3	1		
Burundi			1			
Cape Verde	5					
Cuba		1				
Democratic Republic of Congo		2	1			
Egypt	24		12			
Gaza strip	2					
Georgia	1					
Ghana		1	4			
Israel	160		1			
Italy	2					
Kenya		3	5	1		
Malawi				1		
Nigeria		11				
Reunion Island			2			
Saudi Aarabia			1			
Senegal			2			
Slovenia			1			
Syria			1			
Tanzania			1			
Turkey	1					
Yemen	1					
Zimbabwe		1				

1 Table 3. Number of reports per plant family of *A. swirskii* and *A. rikey* before and after 2005

2 (first commercialisation of *A. swirskii*)

	Bef	fore 2005	l Af	ter 2005
	A. swirkii	A. rikey	A. swirkii	A. rikey
Acanthaceae	1	1		· ·
Actinidiaceae	1			
Adoxaceae	3			
Amaranthaceae	2			
Anacardiaceae	3		5	
Apocynaceae	1		 	
Araceae	+	1		
Arecaceae	1			
Asparagaceae	2			
Brassicaceae	1			
Cannabaceae	+	1		
	3		_	
Caprifoliaceae				
Compositae	11	1		
Convolvulaceae	2	1	-	
Cucubirtaceae	+		1	
Ebenaceae	3			
Equisetaceae	2		<u> </u>	
Euphorbiaceae	4	2	2	
Fagaceae	3			
Geraniaceae	2			
Juglandaceae	2			
Lamiaceae	3	1	2	
Lauraceae	9			
Leguminosae	9	3		
Lythraceae	1			
Malvaceae	8	1	1	
Moraceae	9			
Musaceae		1		
Myrtaceae	6	0	1	
Onagraceae	2			
Passifloraceae			1	
Phyllanthaceae	0		1	
Pinaceae	2			
Poaceae	4	1		
Polygonaceae	2			
Proteaceae		1		
Rhamnaceae	1			
Rosaceae	33		1	
Rubiaceae	1		1	
Rutaceae	27		3	
Salicaceae	2		 	
Solanaceae	10	1	8	
Sapindaceae	2	Τ	+	
Thymelaeaceae	2		-	
Ulmaceae	2		-	
Verbenaceae			1	
	2		11	
Violaceae	2		-	
Vitaceae	7		1	
unknown	5	5	6	3
In Soil			2	
on insect	1			

- 1 Table 4a. Genetic distances (K2P) of 12S rRNA sequences calculated within and between
- 2 Amblyseius swirskii populations here analyzed: mean values (min-max values in brackets)

	Israel	Koppert	Agrobio	Bioplanet	Reunion	Benin introduced E	Benin original	Egypt	Cape Verde
	0.003								
Israel	(0-0.007)								
	0.003	0.0015							
Koppert	(0.003-0.007)	(0-0.003)							
		0.0007							
Agrobio	0.003	(0-0.003)	0						
		0.0007							
Bioplanet	0.003	(0-0.003)	0	0					
	0.0028	0.002	0.002	0.002	0.002				
Reunion	(0-0.1)	(0-0.007)	(0-0.007)	(0-0.007)	(0-0.007)				
	0.002	0.002			0.001				
Benin introduced	(0-0.007)	(0-0.003)	0.003	0.003	(0-0.003)	1			
	0.002	0.002			0.001				
Benin original	(0-0.007)	(0-0.003)	0.003	0.003	(0-0.003)	0	0		
	0.002	0.002			0.001				
Egypt	(0-0.007)	(0-0.003)	0.003	0.003	(0-0.003)	0	0	0	
	0.013	0.013	0.014		0.011	0.010	0.010	0.010	0.011
Cape Verde	(0.007-0.024)	(0.007-0.021)	(0.1-0.21)	0.014 (0.1-0.21)	(0.007-0.021)	(0.007-0.017)	(0.007-0.017)	(0.007-0.017)	(0-0.017)

7 Table 4b. Genetic distances (K2P) of mitochondrial COI sequences calculated within and

between Amblyseius swirskii populations here analyzed: mean values (min-max values in

9 brackets)

	Israel	Koppert	Reunion	Benin introduced	Benin original	Egypt	Cape Verde
	0.001						
Israel	(0-0.002)						
	0.003	0.002					
Koppert	(0-0.005)	(0-0.005)					
	0.003	0.002	0.002				
Reunion	(0.002-0.005)	(0-0.007)	(0-0.007)				
	0.002	0.002	0.002				
Benin introduced	(0.002-0.003)	(0.002-0.007)	(0.002-0.005)	0			
	0.002	0.002	0.002				
Benin original	(0.002-0.003)	(0.002-0.007)	(0.002-0.005)	0		0	
	0.002	0.003	0.003	0.001	0.001	0.001	
Egypt	(0-0.003)	(0.002-0.007)	(0.002-0.005)	(0-0.002)	(0-0.002)	(0-0.002)	
	0.027	0.029	0.029	0.028	0.028	0.028	
Cape Verde	(0.024-0.04)	(0.024-0.042)	(0.022-0.042)	(0.026-0.04)	(0.026-0.04)	(0.024-0.04)	0.014 (0-0.042

Table 4c. Genetic distances (K2P) of mitochondrial CytB sequences calculated within and between *Amblyseius swirskii* populations here analyzed: mean values (min-max values in brackets)

	Israel	Koppert	Syngenta	Reunion	Benin introduced	Benin original	Egypt	Cape Verde
Israel	0.001 (0-0.003)							
	0.008	0.001						
Koppert	(0.006-0.009)	(0-0.006)						
	0.0007	0.005						
Syngenta	(0-0.003)	(0-0.006)	/					
	0.007	0.002	0.006	0.002				
Reunion	(0-0.016)	(0.003-0.013)	(0-0.013)	(0-0.013)				
	0.005	0.010	0.01	0.01	0.002			
Benin introduced	(0.003-0.009)	(0-0.013)	(0.009-0.013)	(0.003-0.019)	(0-0.003)			
	0.006	0.009	0.011	0.011	0.003	0.004		
Benin original	(0.003-0.013)	(0.003-0.016)	(0.009-0.016)	(0.003-0.022)	(0-0.009)	(0-0.013)		
	0.002	0.007	0.002	0.008	0.005	0.006	0.003	
Egypt	(0-0.006)	(0-0.013)	(0-0.006)	(0-0.019)	(0-0.013)	(0-0.016)	(0-0.013)	
	0.028	0.032 (0.019-	0.027	0.032	0.031	0.032	0.028	0.024
Cape Verde	(0.019-0.08)	0.076)	(0.019-0.076)	(0.019-0.076)	(0.022-0.083)	(0.022-0.08)	(0.019-0.083)	(0-0.084)