# Publizierbarer Endbericht

gilt für Studien aus der Programmlinie Forschung

## A) Projektdaten

| Allgemeines zum Projekt | |
|---|---|
| **Kurztitel:** | Climite |
| **Langtitel:** | Potential of the alien biocontrol agent *Amblydromalus limonicus* to become invasive in Austria under climate warming scenarios |
| **Zitiervorschlag:** | Walzer Andreas (2018). Potential of the alien biocontrol agent *Amblydromalus limonicus* to become invasive in Austria under climate warming scenarios. Final report ACRP 2013 (6th call). |
| **Programm inkl. Jahr:** | ACRP 2013 (6th call) |
| **Dauer:** | 46 Monate |
| **KoordinatorIn/ ProjekteinreicherIn:** | Dr. Mag. Andreas Walzer/ Universität für Bodenkultur, Dept. für Nutzpflanzenkunde, Abt. für Pflanzenschutz |
| **Kontaktperson Name:** | Dr. Mag. Andreas Walzer |
| **Kontaktperson Adresse:** | Universität für Bodenkultur, Gregor Mendelstrasse 33, 1180 Wien |
| **Kontaktperson Telefon:** | +43 0147654 95308 |
| **Kontaktperson E-Mail:** | andreas.walzer@boku.ac.at |
| **Projekt- und KooperationspartnerIn (inkl. Bundesland):** | Biohelp GmbH, Kapleigasse 16, Wien (informale Kooperation) Koppert B.V., Holland (informal) IRTA, Dept. of Agriculture, Girona, Spanien (informal) Landcare Research, Lincoln, Neuseeland (informal) INRA, Montpellier, Frankreich (informal) |
| **Schlagwörter:** | Climate warming, alien species, biological control |
| **Projektgesamtkosten:** | 338.605,00 € |

| Allgemeines zum Projekt | |
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| **Fördersumme:** | 338.605,00 € |
| **Klimafonds-Nr:** | KR13AC6K11154 |
| **Erstellt am:** | 26.06.2018 |

# B) Projektübersicht

## 1 Short summary

Üblicherweise können sich exotische Arten bei unbeabsichtigten Freilassungen nicht in ihrer neuen Umgebung etablieren, was auf die einmalige Freilassung in geringer Stückzahl, und der abiotischen und biotischen Resistenz der einheimischen Ökosysteme zurückzuführen ist. Die Verwendung von exotischen Nützlingen zur Schädlingskontrolle im Verbund mit dem Klimawandel können jedoch ideale Bedingungen für die Etablierung und Ausbreitung exotischer Arten schaffen. Erstens wird die Wirksamkeit von Nützlingen in Glashauskulturen oft durch wiederholte Freisetzungen in hoher Stückzahl gefördert, was die Chance einer Etablierung im Freiland erhöht, wenn sie aus dem Glashaus entkommen. Zweitens kann der Klimawandel die abiotische Resistenz einheimischer Ökosysteme durch die Erhöhung der Durchschnittstemperaturen im Winter schwächen, was zu günstigen Überwinterungsmöglichkeiten für exotische Nützlinge in Regionen führen kann, in denen bis dato die vorherrschenden Klimabedingungen kein Überleben im Winter ermöglicht hatten. Wenn bei einem solchen Szenario ein exotischer Nützling eine Kombination von Eigenschaften besitzt, die es erlauben, die biotische Resistenz der einheimischen Lebensgemeinschaften zu überwinden, dann kann ein zuvor harmloser exotischer Nützling zu einer invasiven Art werden.

Der exotische Nützling *Amblydromalus limonicus* (Acari: Phytoseiidae) ist seit 2015 in Österreich als natürlicher Gegenspieler von Thripsen in Glashäusern zugelassen. Der erste Nachweis für das unbeabsichtigte Auftreten von *A. limonicus* im Freiland in Europa stammt aus Spanien (2011), was die Annahme des hohen Etablierungspotentials dieser exotischen Raubmilbe bestätigt. Ziel des Projektes war daher, das Etablierungs- und Invasionspotenzial von *A. limonicus* in Österreich unter aktuellen und zukünftigen Klimabedingungen zu untersuchen. Im Speziellen wurde angenommen, dass (1) die abiotische Resistenz der einheimischen Ökosysteme aufgrund der hohen Temperaturtoleranz von *A. limonicus* und der prognostizierten Temperaturerhöhungen abnimmt und zumindest eine gelegentliche Überwinterung und nachfolgende Etablierung und/oder eine saisonale Etablierung von *A. limonicus* zulässt, (2) *A. limonicus* ein größeres Vermehrungspotenzial hat als einheimische Arten und ein hochaggressiver Räuber ist, was die biotische Resistenz der einheimischen Raubmilbengemeinschaften reduziert, (3) wenn *A. limonicus* in eine einheimische Raubmilbengesellschaft eindringt, dieser exotische Räuber gegenüber den einheimischen Arten dominant sein wird, (4) sich durch den Klimawandel die geeigneten Regionen für die Etablierung von *A. limonicus* in Europa deutlich vergrößern werden.

Zunächst wurde die Temperaturtoleranz von *A. limonicus* untersucht, mit denen die Etablierungswahrscheinlichkeiten des exotischen Nützlings in Österreich unter aktuellen und zukünftigen Temperaturbedingungen abgeleitet werden konnten. Zweitens wurde das Vermehrungspotenzial und die räuberische Aggressivität von

*A. limonicus* gegenüber einheimischen Raubmilbenarten untersucht. Drittens wurden die Auswirkungen einer Einwanderung von *A. limonicus* in eine einheimische Raubmilbengesellschaft untersucht. Schließlich wurde das Verbreitungspotenzial von *A. limonicus* in Europa unter aktuellen und zukünftigen Klimabedingungen Mithilfe von Modelprojektionen (CLIMEX) berechnet.

Die Populationsentwicklung von *A. limonicus* war in einem Temperaturbereich von 10°C bis 30°C gewährleistet, was diese Art als eine wärmeempfindliche, aber kältetolerante Raubmilbe charakterisiert, die aber nicht in der Lage ist, in Diapause zu gehen. Akklimatisierung erhöhte die Kältetoleranz von *A. limonicus*-Weibchen und ermöglichte das Überleben bei 0°C und + 5°C bis zu 6 Wochen bzw. 12 Wochen. Darüber hinaus überlebten akklimatisierte Weibchen unter Freilandbedingungen Kältewellen mit $T_{min}$-Werten bis zu -5°C. Der exotische Räuber war bezüglich Populationswachstum und räuberischer Aggressivität den einheimischen Arten *Euseius finlandicus* und *Kampimodromus aberrans* (Acari: Phytoseiidae) überlegen. *Amblydromalus limonicus* konnte aber keine der beiden einheimischen Arten auf Apfelbäumchen verdrängen, sondern koexistierte mit ihnen über 15 Wochen. Die Modelprojektionen von CLIMEX identifizierten die Küstenregionen im Mittelmeerraum, nicht aber Österreich, als geeignet für die dauerhafte Etablierung von *A. limonicus* sowohl unter aktuellen als auch zukünftigen Klimabedingungen. Durch den Klimawandel sollte sich das potenzielle Verbreitungsgebiet von *A. limonicus* in Europa durch neue geeignete Regionen in den südlichen Teilen von Großbritannien und Irland und entlang der Westküste Frankreichs deutlich erweitern.

Unabhängig vom Klimawandel stellt der exotische Räuber *A. limonicus* ein geringes Invasionsrisiko für österreichische Raubmilbengemeinschaften dar, weil sich der Räuber aufgrund der fehlenden Diapause nicht dauerhaft in Österreich etablieren kann. Auch die gelegentliche Überwinterung mit anschließender Etablierung von *A. limonicus* ist unter den gegenwärtigen klimatischen Bedingungen nicht sehr wahrscheinlich. Der Klimawandel vermindert jedoch die abiotische Resistenz der österreichischen Ökosysteme, wodurch die gelegentliche jährliche Etablierung von *A. limonicus* in Zukunft ermöglicht werden könnte. In einem solchen Szenario könnte *A. limonicus* aufgrund seiner früheren Einwanderung auf Pflanzen im Frühjahr einen Vorteil gegenüber einheimischen Arten haben. Unabhängig von der Klimaerwärmung ist bei einem Entkommen von *A. limonicus* aus Glashäusern mit einer saisonalen Etablierung im Freiland zu rechnen, was normalerweise eine spätere Einwanderung auf Pflanzen als die einheimischen Arten bedeutet. Dieses Szenario wurde in einem Semifreiland-Experiment nachgestellt, wobei der exotische Räuber nicht in der Lage war, die einheimischen Raubmilbenarten auf Apfelbäumchen zu verdrängen. Die Modellprojektionen von CLIMEX bestätigten die Ergebnisse, dass unabhängig vom Klimawandel eine dauerhafte Etablierung der exotischen Raubmilbe *A. limonicus* in Österreich nicht möglich ist. Der Einsatz des exotischen Räubers *A. limonicus* als Nützling in den Mittelmeerländern beinhaltet jedoch das hohe Risiko der dauerhaften Etablierung, da vor allem die Küsten-Regionen als geeignet für *A. limonicus* identifiziert wurden.

# 2 Executive Summary

Most introductions of alien species are not expected to result in invasions, which is commonly attributed to low propagule pressure (a composite measure of the number of individuals per introduction and the frequency of introductions) of the alien species, and the high abiotic and biotic resistance of native ecosystems. The use of alien biocontrol agents and climate warming, however, may create ideal conditions for the establishment and spread of alien species. First, the efficacy of biocontrol agents in greenhouse crops is often promoted by repeated augmentative releases creating a high propagule pressure of the alien biocontrol agent on the native species communities when escaping into the field. Second, climate warming may weaken the abiotic resistance of native ecosystems by the increase of the mean temperatures, which can create favourable abiotic conditions for alien greenhouse biocontrol agents in regions previously prevented from establishing by the prevailing climate conditions. If such a scenario is met by an alien biocontrol agent possessing a combination of biological, ecological and/or behavioural traits allowing to overcome the biotic resistance of the native ecosystem, a previously safe alien biocontrol agent may become an invasive species.

The alien predatory mite *Amblydromalus limonicus* (Acari: Phytoseiidae) is commercially available as natural enemy against thrips species in greenhouses in Austria since 2015. The first record of the unintended occurrence of *A. limonicus* on wild and agricultural plants in Europe comes from Spain in 2011, confirming the assumption of the high invasion potential of this alien biocontrol agent. Thus, the objective of this project was to evaluate the establishment and invasion potential of *A. limonicus* in Austria under present and prospective climate conditions. It was hypothesized that (1) the abiotic resistance of the native ecosystems decreases because of the high temperature tolerance of *A. limonicus* and the predicted temperature increase, which allows at least seasonal or casual annual establishment in mild winters of *A. limonicus*, (2) *A. limonicus* is superior over native species in the capacity for population increase and is a highly aggressive IG predator, which reduces the biotic resistance of native predatory mite communities, (3) *A. limonicus* becomes dominant when invading an ecosystem occupied by an established native predatory mite guild, (4) and climate warming dramatically increases the appropriate regions for invasion of *A. limonicus* in Europe.

First, we evaluated the temperature tolerance of *A. limonicus*, which allowed predetermining the establishment probabilities of *A. limonicus* in Austria under present and prospective temperature regimes. Second, we evaluated the capacity for population increase and the performance of *A. limonicus* as intraguild (IG) predator against the native phytoseiid mite species. Third, we simulated in a semi-field experiment an escape of *A. limonicus* from greenhouses to outdoor plants occupied by native phytoseiid species. Finally, we developed distribution maps of *A. limonicus* under present and predicted temperature regimes.

Population development of *A. limonicus* is ensured within a temperature range of 10°C to 30°C with a thermal optimum around 27°C, characterizing this species as a heat-sensitive, but cold-tolerant phytoseiid mite species that is not able to enter diapause. Acclimatization increased the cold-tolerance of *A. limonicus* females allowing the survival up to 6 weeks at permanent 0°C and 12 weeks at permanent +5°C. Furthermore, acclimatized females survived under field conditions cold waves with $T_{min}$ values up to -5°C, but not below this value. The alien predator was superior in population growth and intraguild predation (IGP) over native species, however, heat stress lowered the IGP risk posed by *A. limonicus*. In the semi-field experiment, *A. limonicus* did not eliminate any of the two native species, but co-existed with them over 15 weeks. The model projections of CLIMEX identified the coastal regions in the Mediterranean Basin, but not Austria, as suitable for permanent establishment of *A. limonicus* both under present and prospective climate conditions. Climate warming should expand the range of *A. limonicus* in Europe with novel suitable regions in the southern parts of Great Britain and Ireland and along the west coast of France.

Summing up, the alien predator *A. limonicus* should pose a low invasion risk for Austrian predatory mite communities irrespective of climate warming, because (1) the alien predator is not able to establish permanently in Austria due to the lack entering diapause; (2) also permanent establishment of the alien predator in a novel region (north-eastern Spain since 2011) had no negative effects on the native predatory mite community; and (3) seasonal establishment did not result in the elimination of native species. Casual annual establishment of *A. limonicus* is also not very likely under present climate conditions. Not a single female survived the last two winters in the field, although the mean temperatures were relatively high (+0.37°C and +2.17°C). Climate warming, however, lowers the abiotic resistance of Austrian ecosystems, which may allow the casual overwintering and subsequent establishment of *A. limonicus* in the future. In such a scenario, *A. limonicus* may have a benefit over native species because of its earlier arrival on plants in spring. Independent of climate warming, seasonal establishment of *A. limonicus* is likely in case of escaping into the field during the growing season, which usually means a later arrival on plants than native species. Independent of climate warming, the model projections of CLIMEX confirmed the findings that permanent establishment of the alien predatory mite *A. limonicus* is not possible in Austria. However, an application of the alien predator *A. limonicus* as biocontrol agent in Mediterranean countries includes the high risk of the permanent establishment, because these regions were identified as suitable for *A. limonicus*. Nonetheless, it is strongly recommended to continue investigations on the priority effects (the order in which species arrive into a community) on the establishment and invasion success of *A. limonicus* in Austrian predatory mite communities.

# 3 Background and objectives

Climate warming and invasive species currently pose two of the most important ecological challenges worldwide. Although these two factors are known to be tightly linked, they are often viewed independently. However, climate warming may create optimal conditions for alien species in regions, where these species were previously not able to survive.

The main objective was to evaluate the establishment and invasion potential of a greenhouse biocontrol agent, the predatory mite *Amblydromalus limonicus* (Acari: Phytoseiidae), in Austria under present temperature conditions and under temperature conditions predicted by IPCC for 2100. We hypothesized that *A. limonicus* has traits that allow its invasion into native Austrian plant-inhabiting mite communities under climate warming. *Amblydromalus limonicus* is an alien predator originating from temperate and sub-tropical regions in America, Australia and New Zealand and commercially available since 2015 in Austria for thrips control in greenhouse crops. The first unattended record of *A. limonicus* in the open field comes from Nord-eastern Spain in 2011, where *A. limonicus* was found at three locations in high population densities, indicating its potential for invasion.

The specific hypotheses were that (1) *A. limonicus* is well able to cope with the prevailing abiotic resistance of Austrian ecosystems because of its high temperature tolerance and the predicted temperature rise allows at least its seasonal or casual establishment in mild winters in Austria, (2) the ability to invade and establish in Austria differs among strains of *A. limonicus*, (3) *A. limonicus* is superior over native phytoseiid species in the capacity for population increase and is a highly aggressive IG predator, allowing to cope with the biotic resistance of the native predatory mite communities, (4) *A. limonicus* becomes a dominant species when invading plants occupied by an established native predatory mite guild, and (5) climate warming dramatically increases the regions appropriate for invasion of *A. limonicus* in Europe.

We performed five work packages (WP) to test our hypotheses. WP 1 was concerned with localization, sampling and identification of three *A. limonicus* strains and three native phytoseiid mite species. Additionally, we evaluated the IG aggressiveness of the alien predatory mite *A. limonicus* and the native predatory mite *Amblyseius andersoni* (Acari: Phytoseiidae) collected in north-eastern Spain, where *A. limonicus* is well established since 2011. In WP 2 we evaluated the temperature tolerance of *A. limonicus*, which allowed pre-determining the establishment probabilities of *A. limonicus* in Austria (seasonal establishment during the growing season, casual establishment in years with mild winter, permanent establishment) under present and predicted temperature regimes. Based on the results of WP 2 we determined the *A. limonicus* strain with the highest probability to survive at low temperatures. This strain was used in all further experiments. In WP 3 we evaluated the capacity for population increase of *A. limonicus* and its performance as IG predator of native phytoseiid mite species. These traits are important for invaders to cope with the biotic resistance of native communities. Additionally, we evaluated learning effects on the

antipredator behaviour of native predatory mites against the alien predator. In WP 4 we simulated in semi-field experiments the dispersal of *A. limonicus* from greenhouse crops to outdoor plants occupied by native phytoseiid species. Finally, in WP 5 we developed distribution maps of *A. limonicus* under present and predicted temperature regimes in 2100 using the software CLIMEX.

# 4 Results

**WP1**

*Intraguild aggressiveness between an alien predatory mite and its native opponent*

Intraguild (IG) predator and prey behavior
The IG aggressiveness functions of the IG predators differed significantly between the two predator species (Kaplan-Meier analysis, Breslow tests: $\chi^2_1 = 10.164$, p = 0.001). The alien IG predator *A. limonicus* was more aggressive than the native predator *A. andersoni*, which was reflected in earlier attacks (mean attack times of *A. limonicus*: 48.31 min ± 7.54 SE versus *A. andersoni*: 103.78 ± 5.55) and more frequent attacks on IG prey larvae (Fig. 1).
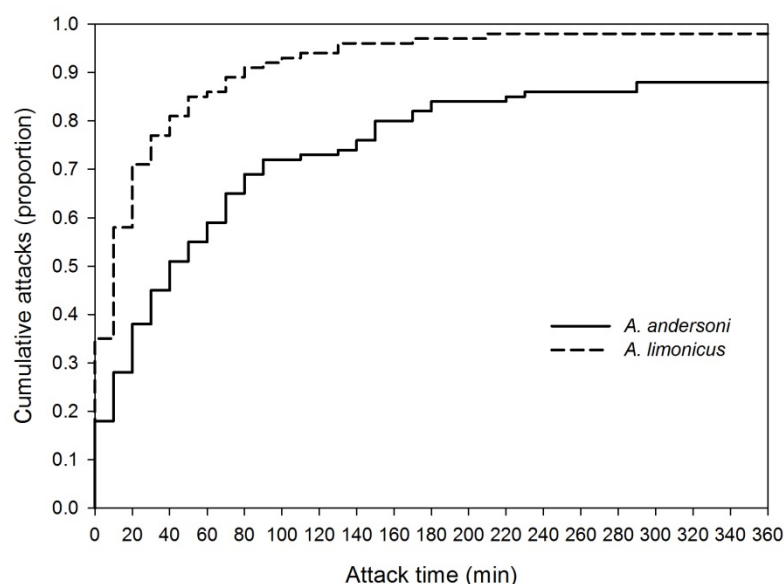


Fig. 1. The intraguild (IG) attack functions (combined parameter of cumulative attacks and attack times) of the alien predator *A. limonicus* and the native predator *A. andersoni*, when preying on each other (IG predators: females, IG prey: larvae) over 360 min.

Both IG predator and prey activity were not influenced by species affiliation (Fig. 2), but prey survival ($\chi^2_1 = 7.106$, p = 0.008) and IGP success ($\chi^2_1 = 4.481$, p = 0.034). Survival probabilities of the native IG prey were negligible in contrast to

the alien IG prey, because nearly all alien IG predators attacked the IG prey within 360 min in contrast to the native IG predator (*A. limonicus*: 69 out of 71; *A. andersoni*: 65 out of 74). Additionally, the alien species *A. limonicus* had a higher IGP success than the native species *A. andersoni*. Nearly all attacked native IG prey larvae were killed by the alien predator females, whereas about 10% of the alien IG prey larvae survived the attacks of the native IG predator (Fig. 2).
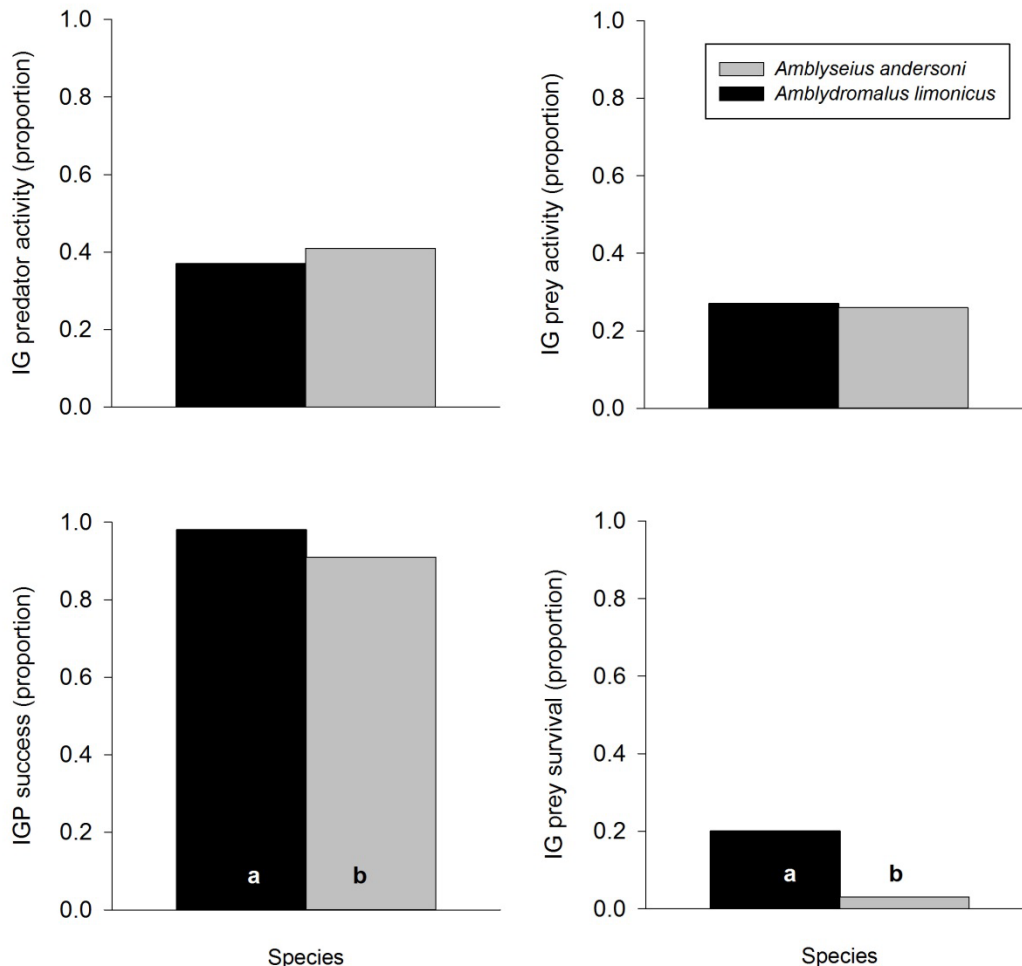


Fig. 2. IG predator activity, IG prey activity, IG predation success and IG prey survival of *A. limonicus* and *A. andersoni*, when acting as IG predator (female) or IG prey (larva) over 360 min.

IG predator and prey body sizes

The IG predator females of *A. limonicus* and *A. andersoni* were similarly sized; however, IG larval prey sizes differed between the alien and native species ($\chi^2_1$ = 13.343, p < 0.001). The alien IG prey was larger than the native IG prey. Consequently, also the IG predator/prey body size ratio of the alien predator and native prey was larger than the corresponding data of the native predator and alien prey (Fig. 3).
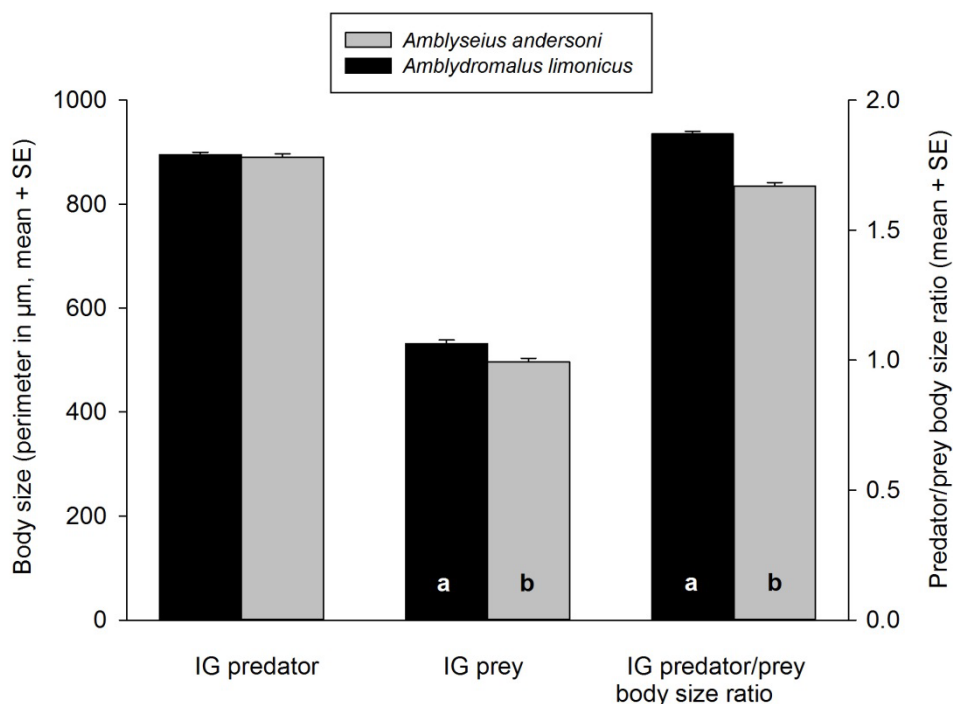
Fig. 3. Body size of *A. limonicus* and *A. andersoni* as IG predator (females) or IG prey (larvae), and the predator/prey body size ratios.

## WP2

*Temperature effects on survival, age and size at maturity and fecundity*

### Survival

Irrespective of population, permanent heat stress (35 °C) resulted in the desiccation of all eggs. Juvenile survival between 10°C and 30°C was affected by temperature (GLM, $X^2_4=22.995$; p=0.007), but not population and their interaction. Juvenile survival probabilities were lower at 10°C than at other temperatures. Only temperature influenced the survival of the females (GLM, $X^2_1=7.292$; p=0.007). All females survived the experimental period of 10 days at 10°C, 15°C and 20°C. At higher temperatures the survival probabilities of the females decreased (at 25°C = 0.90 (proportion); at 30°C = 0.69). Permanent heat stress at 35°C resulted in the death of all females within 3 days.

### Age at maturity

All main factors (population: $X^2_2=17.260$; p<0.001, temperature: $X^2_4=9140.672$; p<0.001; sex: $X^2_1=9.646$, p=0.002) influenced the age at maturity. Juveniles derived from the NZ population reached later maturity than SP and KO individuals. Juveniles developed faster with increasing temperatures up to 30°C. Males developed faster than females. Additionally, the effect of temperature on the age at maturity was dependent on the population affiliation ($X^2_8=55.554$; p<0.001). At 10°C, individuals from the NZ population reached later maturity than individuals from the SP and KO populations. Furthermore, the effect of

temperature was dependent on sex ($X^2_4=11.809$; p=0.019). Males developed faster only at low temperatures (Fig. 4A, B).

Size at maturity

The statistical analyses revealed that the individuals reached their largest and smallest body sizes at 15°C and 30°C, respectively (GLM: $X^2_4=545.309$; p<0.001) and males were smaller than females ($X^2_1=7805.605$; p<0.001). Females and males, however, responded differently to temperatures (temperature x sex: $X^2_4=64.291$; p<0.001). Male body size decreased with increasing temperatures, whereas female body size first peaked at 15°C and then decreased with increasing temperatures (Fig. 4C, D).
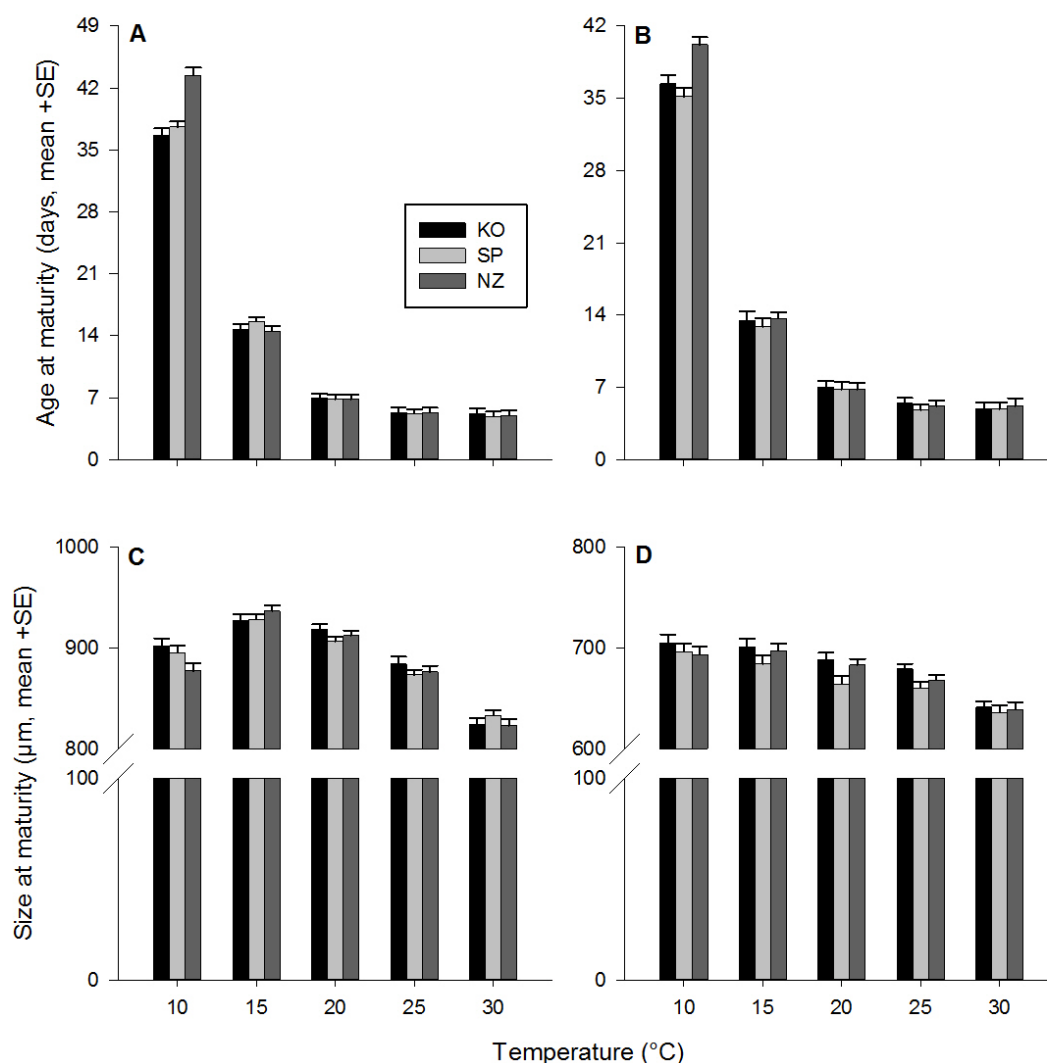


Fig. 4. Temperature effects on age (A, B) and size (C, D) at maturity in females (A, C) and males (B, D) deriving from three *A. limonicus* populations [KO= koppert (commercial producer of natural enemies); SP=Spain, Girona (alien population); NZ= New Zealand, Auckland (native population)].

Fecundity

Egg production of *A. limonicus* was affected by temperature (GLM, $X^2_5=1436.597$; p<0.001) and population ($X^2_2=64.628$; p<0.001). Pooled over populations, egg production increased with temperatures until 25°C and dropped

at 30°C. At 35°C, egg production was nearly zero. Pooled over temperature, the ranking of the egg production was the following: SP > KO > NZ. The interaction of temperature and population was also significant ($X^2_{10}=87.134$, $p<0.001$). The SP females produced more eggs at 20°C, 25°C and 30°C than KO and NZ females (Fig. 5).
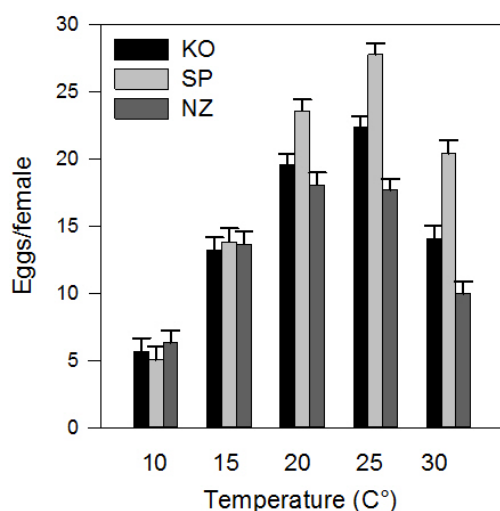


Fig. 5. Temperature effects on female reproductive success deriving from three *A. limonicus* populations [KO= koppert (commercial producer of natural enemies); SP=Spain, Girona (alien population); NZ= New Zealand, Auckland (native population)].

*Diapause*

Irrespective of population, none of the *A. limonicus* females were able to enter diapause. Contrary, all *E. finlandicus* females stopped egg production at winter conditions and restarted egg production at spring conditions indicating the ability of entering diapause.

*Cold tolerance and thermal plasticity*

Irrespective of acclimatization, all females died within 3 days at -5°C. Acclimatized females survived up to 55 days at 0°C (Kaplan-Meier analysis, Breslow tests: $X^2_1=97.295$; $p<0.001$) (Fig. 6A). Irrespective of acclimatization, most females survived the period of 12 weeks at 5°C and 15°C Fig. (6B, C). Pooled over acclimatization, females produced more eggs at +15°C (GLM, $X^2_1=170.257$; $p<0.001$). Irrespective of temperature, acclimatized females produced more eggs than non-acclimatized females (GLM, $X^2_1=37.360$; $p<0.001$). Pooled over acclimatization, egg hatchability at +15°C was significantly lower for eggs produced at 5°C than at 15°C ($X^2_1=345.824$; $p<0.001$). Pooled over temperature, egg hatchability at +15°C was significantly lower for eggs produced by non-acclimatized females ($X^2_1=3.914$; $p=0.048$) (Fig. 6D).
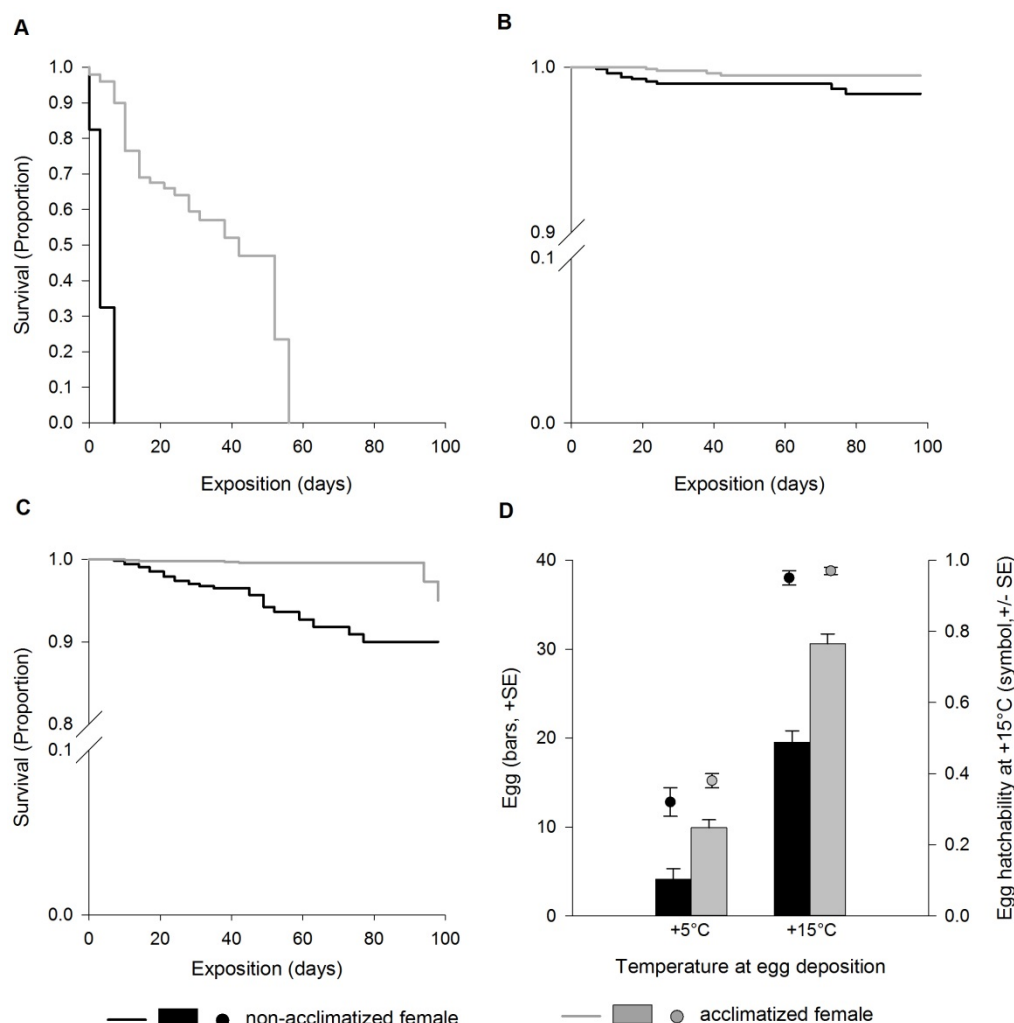
Fig. 6. The survival functions (combination of survival time and proportion) of acclimatized and non-acclimatized *A. limonicus* females exposed to 0°C (A), 5°C (B) and 15°C (C) and the number of deposited eggs at 5°C and 15°C and their egg hatchability rates at 15°C (D).

*Winter survival under natural thermal conditions in Eastern Austria*

The temperature profile in 2016/17 clearly indicated that the placement of the closable cages in the ground vegetation layer had a thermal buffering effect by cutting the daily maximum and minimum temperature peaks about 2-4°C compared to the ambient temperatures. Both *A. limonicus* and *E. finlandicus* survived three cold periods in December with daily minimum temperatures up to -5°C, however, the survival probabilities were significantly higher for the native *E. finlandicus* (Kaplan-Meier analysis, Breslow tests: $X^2_1 = 16.937$, $p < 0.001$). The minimum temperatures during the next cold period at the beginning of January reached -11°C in the ground vegetation layer, which resulted in the death of all predatory mites (Fig. 7).
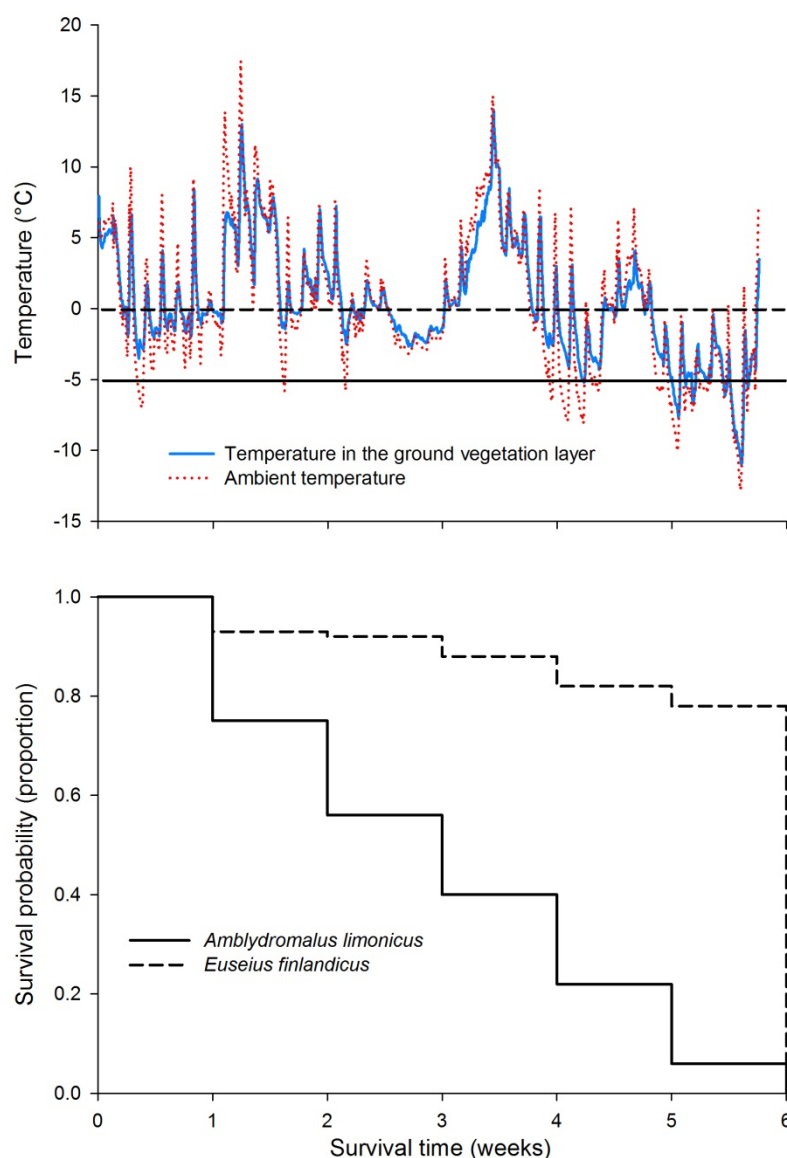
Fig. 7. Temperature profile in the ground vegetation layer and air, and the survival functions of the alien predator *A. limonicus* and native predator *E. finlandicus* in the winter period 2016/17.

In general, the winter temperatures in 2017/18 were milder than in 2016/17 up to the third week of February and both species survived 12 weeks in high densities. The Kaplan-Meier analysis (Breslow tests: $X^2_1 = 24.042$, p < 0.001), however, indicated that the survival probabilities of the native species *E. finlandicus* were higher than of the alien species *A. limonicus* [0.95 (proportion) versus 0.65]. Afterwards the temperatures in the ground vegetation layer decreased up to -13°C, which resulted again in the death of all females (Fig. 8).
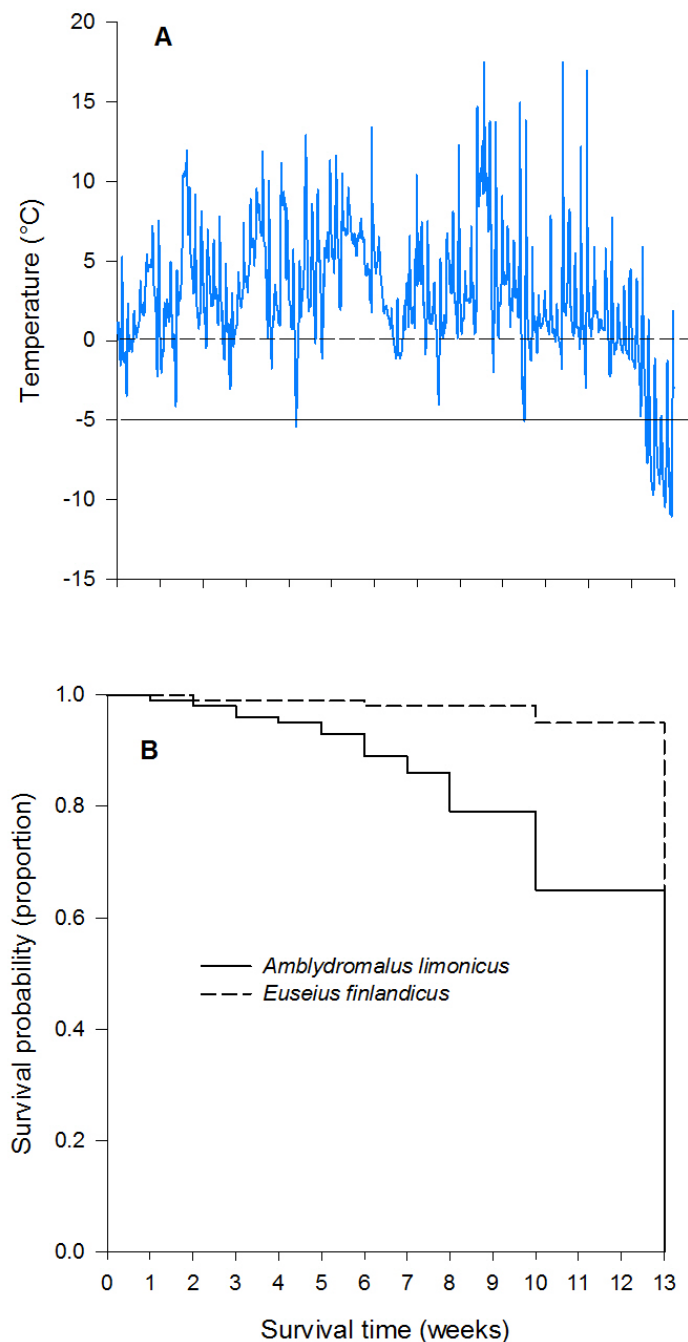
Fig. 8. Temperature in the ground vegetation layer (A), and the survival functions of the alien predator *A. limonicus* and native predator *E. finlandicus* (B) in the winter period 2017/18.

*Intra- and trans-generational plasticity induced by heat waves*

These experiments were conducted for two reasons: (1) to solve the paradox that *A. limonicus* is able to survive in North-eastern Spain under extreme hot summer conditions, but no individual survived at constant +35°C in the lab; (2) to evaluate the intra- and inter-generational plasticity potential of *A. limonicus*, when exposed to heat waves (fluctuating temperatures).

## Intra-generational plasticity effects

Contrary to permanent heat stress at 35°C, survival (proportion) of offspring *A. limonicus* was high and not affected by $T_{max}$ ($T_{max}$ 35°C: 0.88, $T_{max}$ 30°C: 0.90). Size at maturity was affected by $T_{max}$ (GLM, $X^2_1=4.429$, p=0.035), and sex ($X^2_1=317.710$, p>0.001). Body size decreased at higher $T_{max}$ and the daughters were larger than sons. The effects of sex, however, were dependent on $T_{max}$ ($X^2_1=6.132$, p=0.013). Female, but not male body size, decreased at higher $T_{max}$. Age at maturity was only influenced by the main factors $T_{max}$ (GLM, $X^2_1=4.247$, p=0.039) and sex ($X^2_1=6.916$, p=0.009). *Amblydromalus limonicus* reached later adulthood at higher $T_{max}$ and sons developed faster than daughters.


## Inter-generational plasticity effects

Irrespective of offspring temperatures ($T_{offspring}$), all juveniles reached adulthood, when derived from parents reared at 30°C. Also juvenile survival was not affected by $T_{offspring}$, when derived from parents reared at 35°C ($T_{offspring}$ = 35°C: 0.83 (proportion), $T_{offspring}$ = 30°C: 0.90).  Male and female offspring size at maturity were affected by $T_{offspring}$ (males: $X^2_1=4.233$, p=0.040; females: $X^2_1=4.777$, p=0.029). Offspring were larger, when exposed to common summer conditions. Additionally, female size was also affected by the interaction of $T_{offspring}$ and parental temperatures ($T_{parental}$) ($X^2_1=25.758$, p>0.001). Female offspring reached larger sizes, when $T_{offspring}$ and $T_{parental}$ matched. Irrespective of sex, age at maturity was only affected by $T_{parental}$. Pooled over $T_{offspring}$, both male and female offspring deriving from parents exposed to heat stress reached earlier adulthood than offspring derived from parents exposed to common summer conditions (males: $X^2_1=6.166$, p=0.013; females: $X^2_1=10.722$, p>0.001).


## WP3

*Capacity for population increase*

The pairwise comparisons within each temperature among the three populations indicated that the capacity for population increase was significantly higher for the SP population at higher temperatures (20°C, 25°C, 30°C) than the corresponding data of the KO and NZ populations (all pairwise P-values <0.01) (Fig. 9).
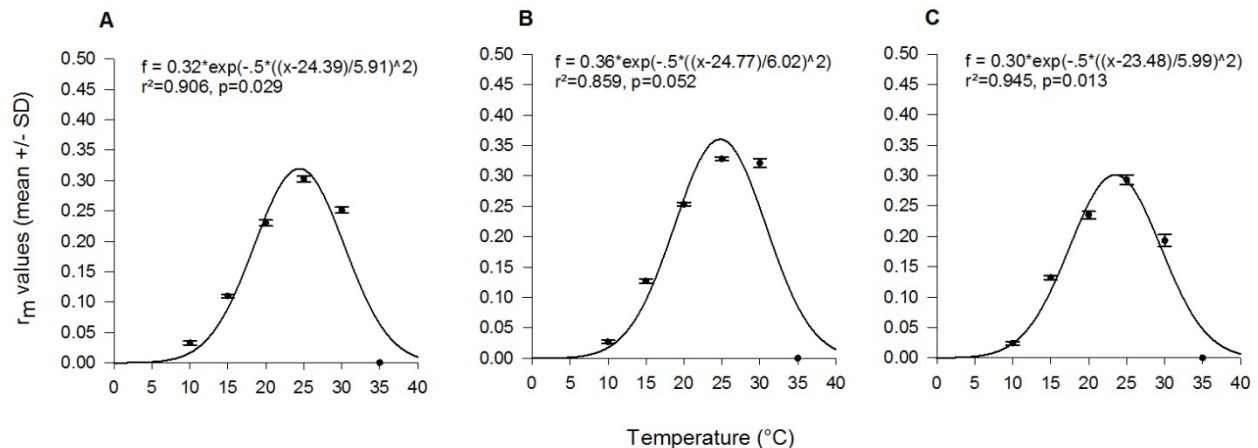
Figure 9. The capacity for population increase ($r_m$-values) of three *A. limonicus* populations [A= koppert (commercial producer of natural enemies); B=Spain, Girona (alien population); C= New Zealand, Auckland (native population)] regressed on temperature.

*Categorization of native and alien IG prey and predators*

IG prey survival

Pairwise comparisons between the temperatures indicated the survival probabilities and survival times of the alien IG prey *A. limonicus* decreased with increasing temperatures independent of predator species (pairwise Breslow tests, IG predator *E. finlandicus*: 26°C vs. 32°C: p = 0.049; IG predator *K. aberrans*: 26°C vs. 32°C: p = 0.048). Irrespective of temperature, *E. finlandicus* was the more dangerous IG predator for the alien IG prey *A. limonicus* (all pairwise comparisons: p > 0.05) (Fig. 10).

The survival probabilities and survival times of the native IG prey species *E. finlandicus* (p = 0.043) and *K. aberrans* (p > 0.001) were higher at 32° than 26°C, when confronted with the alien predator. The survival of *E. finlandicus* was not affected by temperature, when confronted with the native predator *K. aberrans*. Irrespective of temperature, survival functions of *E. finlandicus* larvae were lower when confronted with alien predator *A. limonicus* (all pairwise comparisons: p > 0.05), whereas survival functions of *K. aberrans* were not affected by IG predator species (Fig. 10). Summing up, the alien predator posed to be a high-risk IG predator for both native species.
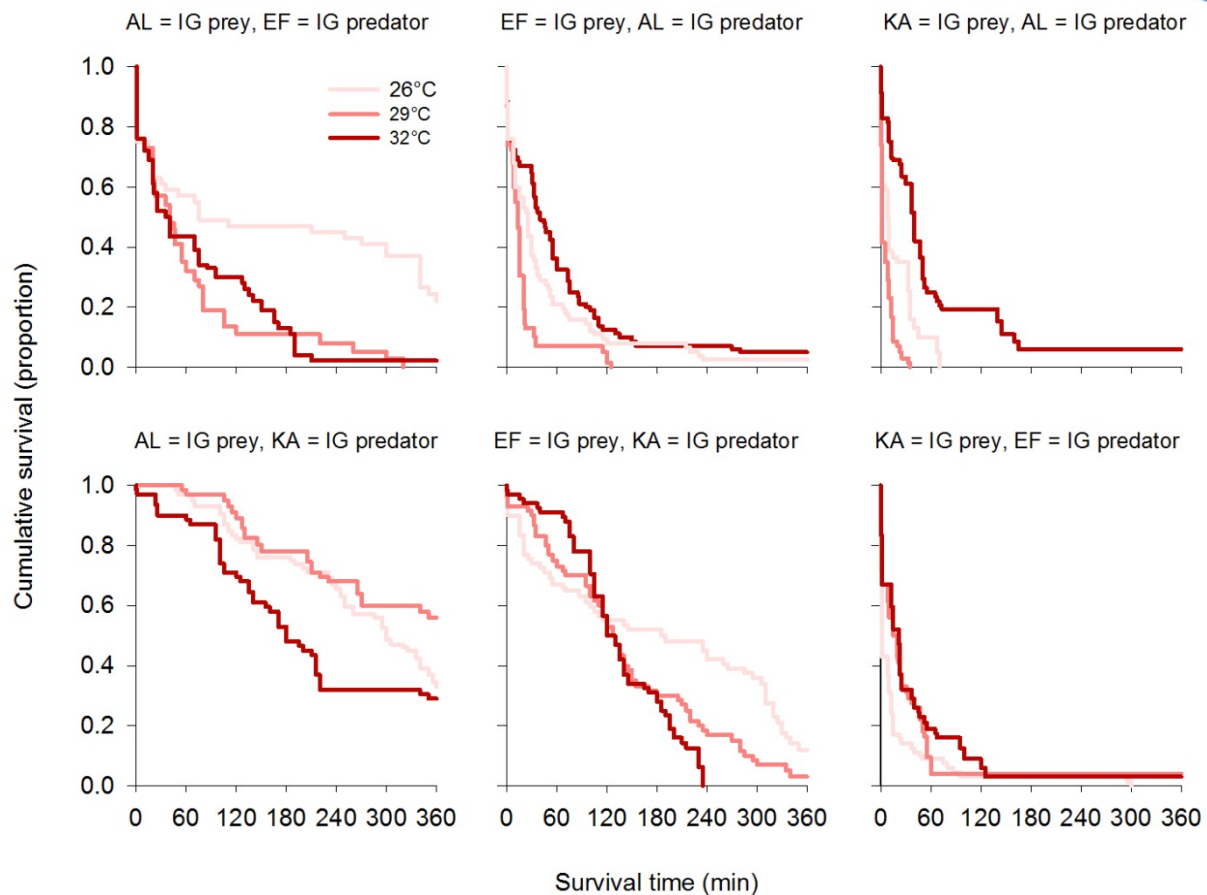
Fig. 10. Temperature dependent survival functions (combination of cumulative survival and survival time) of single IG prey larvae of *A. limonicus* (A, D), *E. finlandicus* (B, E) and *K. aberrans* (C, F), when confronted with a single IG predator female of *A. limonicus* (B, C), *E. finlandicus* (A, F) or *K. aberrans* (D, E) over 6h (Kaplan-Meier analyses, Breslow tests, pooled over IG predators: *A. limonicus*: $X^2_2=6.584$, p=0.037; *E. finlandicus*: $X^2_2=5.881$, p=0.053; *K. aberrans*: $X^2_2=26.812$, p>0.001; pooled over temperatures: *A. limonicus*: $X^2_1=58.515$, p>0.001; *E. finlandicus*: $X^2_1=71.404$, p>0.001; *K. aberrans*: $X^2_1=1.028$, p=0.311).

When the alien IG predator *A. limonicus* started an attack on IG prey, the predation success ranged between 0.96 and 0.99 (proportion) and was not affected by prey species, temperature or their interaction (Fig. 11A). The predation success of the native IG predator *E. finlandicus* was influenced by temperature (GLM, $X^2_2=9.626$, p=0.008), IG prey species ($X^2_1=12.286$, p>0.001) and their interaction ($X^2_2=9.626$, p=0.008). Pooled over IG prey species, predation success of *E. finlandicus* increased from 0.90 at 26°C to 0.98 at higher temperatures. Pooled over temperature, predation success was higher on the native than alien IG prey (0.91 versus 0.99). However, predation success of *E. finlandicus* on native IG prey was not affected by temperature, whereas *E. finlandicus* was able to overwhelm and kill more *A. limonicus* larvae at higher temperatures (29°C, 32°C) (Fig. 11B). The predation success of the second native IG predator species, *K. aberrans*, was influenced only by prey species

($X^2_1$=24.892, p>0.001). *Kampimodromus aberrans* overwhelmed and killed more native than alien IG prey (Fig. 11C).
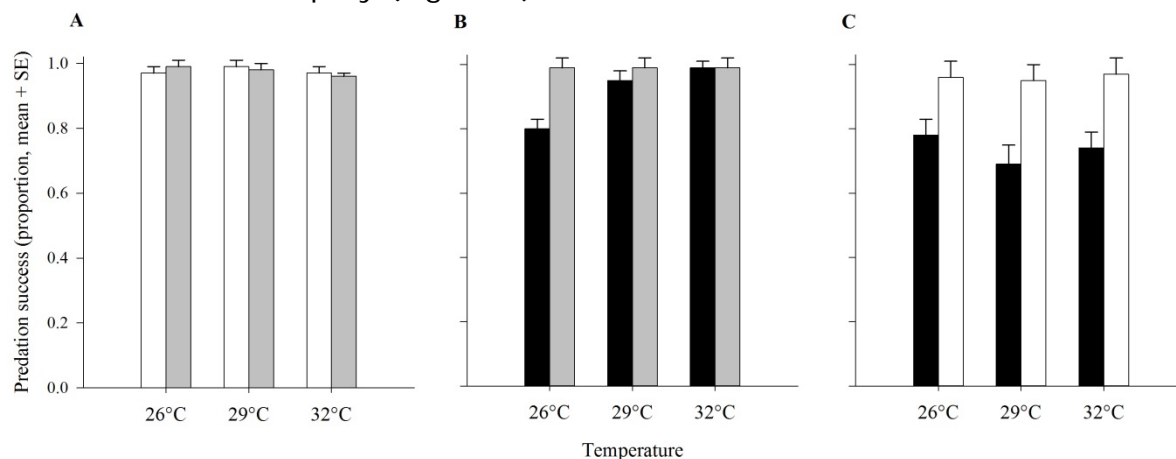


Fig. 11. Temperature dependent predation success of single IG predator females of *A. limonicus* (A), *E. finlandicus* (B) and *K. aberrans* (C), when provided with single IG prey larvae (*A. limonicus*: black bars, *E. finlandicus*: white bars, *K. aberrans*: grey bars) over 6h.

*Learning effects on the interaction of native IG prey and alien predator*

IG predation

The alien predator *A. limonicus* were only provided with naïve IG prey, because there were no juveniles of *K. aberrans* available, when *K. aberrans* females were reared together with the alien predator *A. limonicus*. Both egg production (naïve predators: 1.40 eggs per female + 011SE, experienced predators: 1.42+0.10; GLM, $X^2_1$=0.028, p=0.868) and IG predation (naïve predators: 19.05 IG prey per female per day + 0.42SE, experienced predators: 18.76 +0.40; GLM, $X^2_1$=0.249, p=0.618) of the alien predator *A. limonicus* were not affected by the predator experience. Contrary, all *K. aberrans* females did not produce eggs in the presence of IG prey. The IG predation rates of *K. aberrans*, however, were influenced by predator experience ($X^2_1$=77.010, p>0.001), prey experience ($X^2_1$=16.359, p>0.001) and their interaction ($X^2_1$=12.355, p>0.001). Pooled over prey experience, naïve predators killed more IG prey than experienced predators (1.81 IG prey per female per day ±0.12SE versus 0.26 ±0.13). Pooled over predator experience, experienced IG prey was less often killed than naïve IG prey (1.39 ± 0.11 versus 0.68 ± 0.14). This IG prey experience effect was only detectable, when IG prey was exposed to naïve predators (experienced IG prey: 1.14 ± 0.20, naïve prey: 2.48 ± 0.11).

Oviposition site selection

The oviposition site selection of *K. aberrans* was marginally influenced by female experience (GLM, $X^2_1$=3.547, p=0.060). Pooled over time, naïve females preferred the IG predator free prey patches for oviposition [0.66 (proportion) versus 0.42]. Time also affected the oviposition site selection ($X^2_1$=6.329, p=0.011). Pooled over experience, *K. aberrans* females preferred the IG predator free prey patches for oviposition after 48h (0.67) (Fig. 12A, B). Oviposition site

selection of *A. limonicus* was only affected by time ($X^2_1$=5.346, p=0.021). Pooled over experience, *A. limonicus* females preferred the prey patches with IG predator cues for oviposition after 48h (0.61) (Fig. 12D, E). IGP on predator eggs and larvae of *K. aberrans* females was affected by experience ($X^2_1$=19.878, p>0.001) and time ($X^2_1$=12.807, p>0.001). Pooled over time, naïve females did not prey on predator eggs and larvae in contrast to experienced females (0.64 IG prey + 0.12 SE per female). The IGP rates of the experienced *K. aberrans* females increased over time (24h: 0.21 + 0.06, 48h: 0.43 + 0.07) (Fig. 12C). The IGP rates of the *A. limonicus* females were only affected by the main factors experience ($X^2_1$=12.179, p>0.001) and time ($X^2_1$=38.701, p>0.001). Pooled over time, naïve females killed more IG prey than experienced females (2.39 + 0.13 versus 1.63 + 0.14). Pooled over experience, more IG prey was killed after 48h (2.51 + 0.09 versus 1.52 + 0.12) (Fig. 12F).
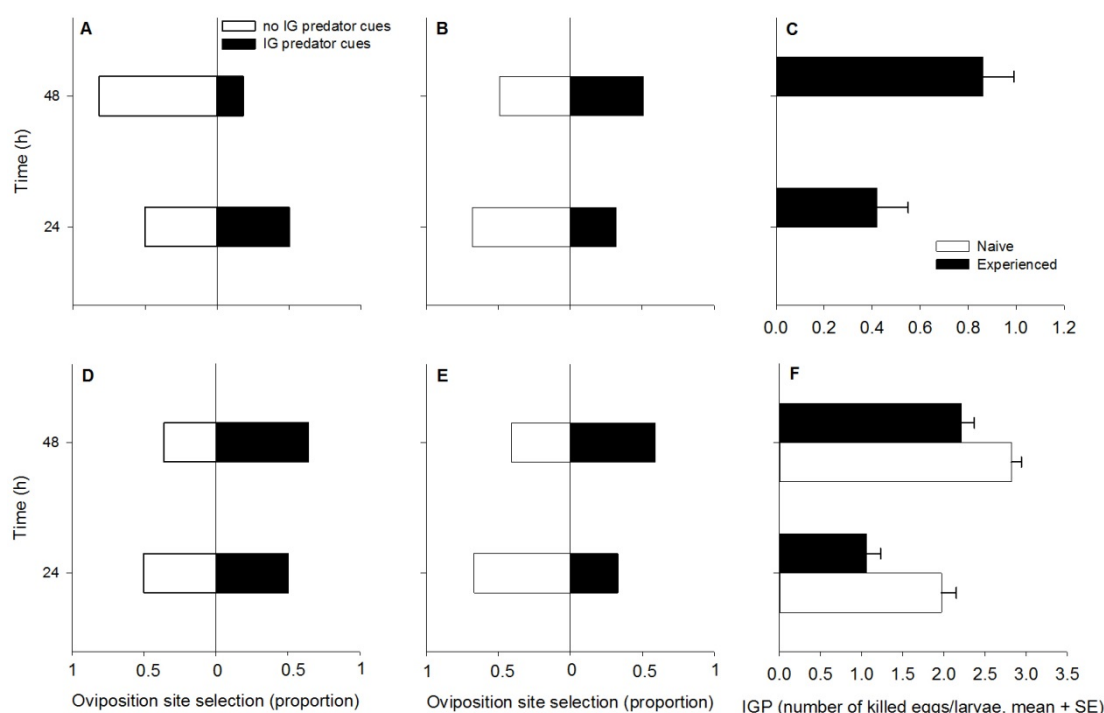


Fig. 12. Oviposition site selection of single, naïve (A, C) and experienced (B, D) *K. aberrans* (A, B) and *A. limonicus* (D, E) females after 24 and 48h, when having the choice between prey patches with or without IG predator cues (predator traces and eggs). Intraguild predation (IGP) of single, naïve and experienced *K. aberrans* (C) and *A. limonicus* (F) females in the prey patch with IG predator cues.

## WP4

*Establishment potential of A. limonicus in the field*

Population development
Generalized estimation equations (GEE's) revealed that population development of the native *K. aberrans* was not affected by the presence of the exotic predator

*A. limonicus*, but by the stratum ($X^2_1$=18.883, p>0.001) and time ($X^2_{14}$=71.823, p>0.001). Population densities increased over time and more *K. aberrans* were found on the upper stratum. However, the significant interaction ($X^2_{14}$=53.500, p>0.001) among treatment, stratum und time indicated that *K. aberrans* shifted earlier from the lower to the upper stratum in the presence of *A. limonicus* (Fig. 13).
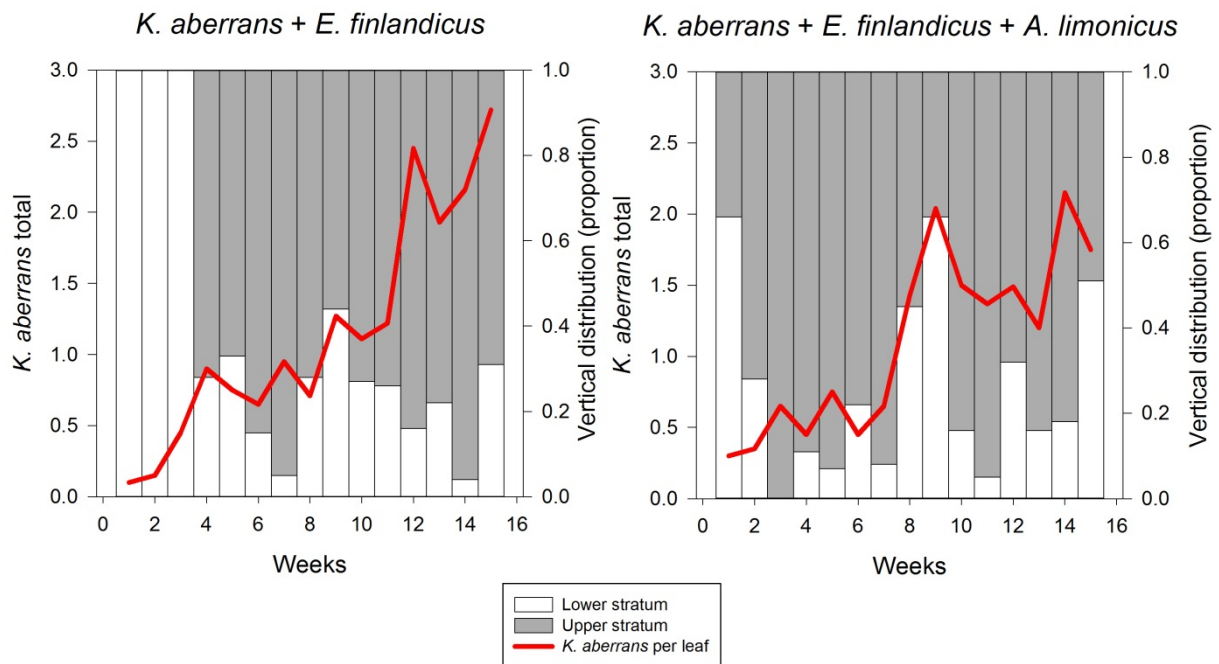


Figure 13. Population development and vertical distribution of native *K. aberrans* in a two species system (*K. aberrans + E. finlandicus*) and three species system (*K. aberrans + E. finlandicus + A. limonicus*) over 15 weeks.

The population development of the second native species *E. finlandicus* was affected by the treatment ($X^2_1$=10.869, p=0.001) and time ($X^2_{14}$=99.132, p>0.001), but not stratum. The population densities of *E. finlandicus* were significantly lower in the presence of the exotic predator *A. limonicus* and the number of *E. finlandicus* increased until week 10 and declined then until the end of the experiment. The significant three way interaction ($X^2_{14}$=27.886, p=0.015) indicated that more *E. finlandicus* were found in the upper stratum in weeks 12 and 13 in the presence of *A. limonicus*, whereas *E. finlandicus* was similarly distributed in both strata in the absence of *A. limonicus* (Figure 14).
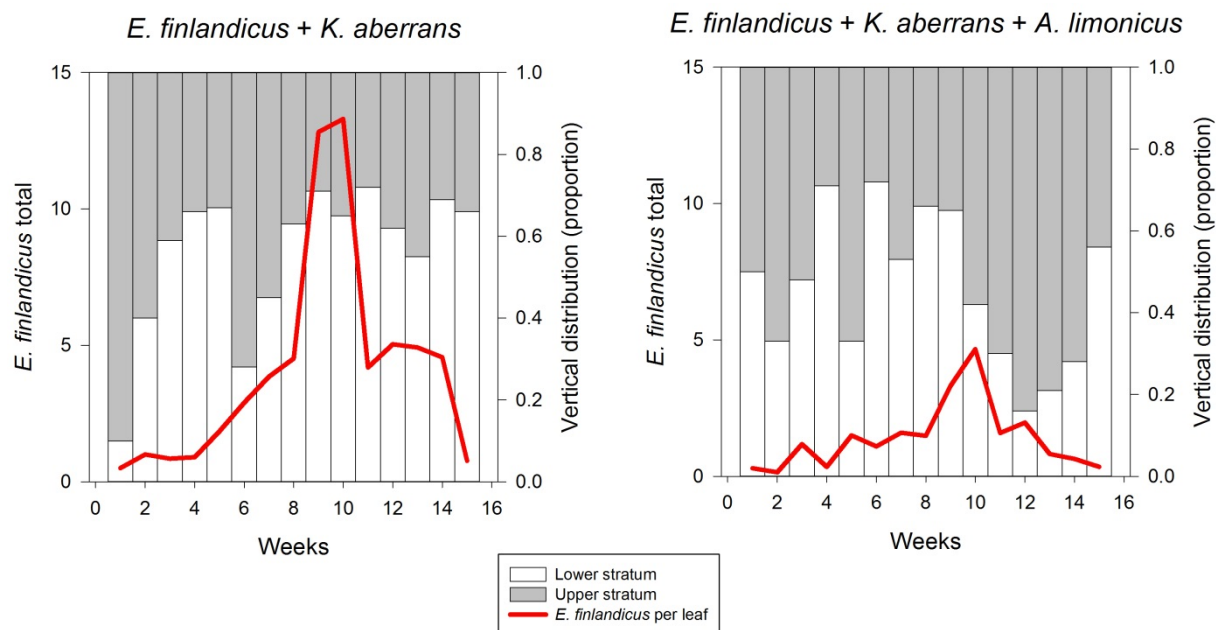
Figure 14. Population development and vertical distribution of native *E. finlandicus* in a two species system (*E. finlandicus + K. aberrans*) and three species system (*E. finlandicus + K. aberrans + A. limonicus*) over 15 weeks.

The population development of *A. limonicus* was only affected by time ($X^2_{14}$=174.143, p>0.001). The densities of *A. limonicus* peaked at week 10 and decreased then slowly until the end of the experiment. *Amblydromalus limonicus* migrated earlier in the upper stratum in the absence of the native predatory mite species (three way interaction: $X^2_1$=35.001, p=0.001) (Figure 15).


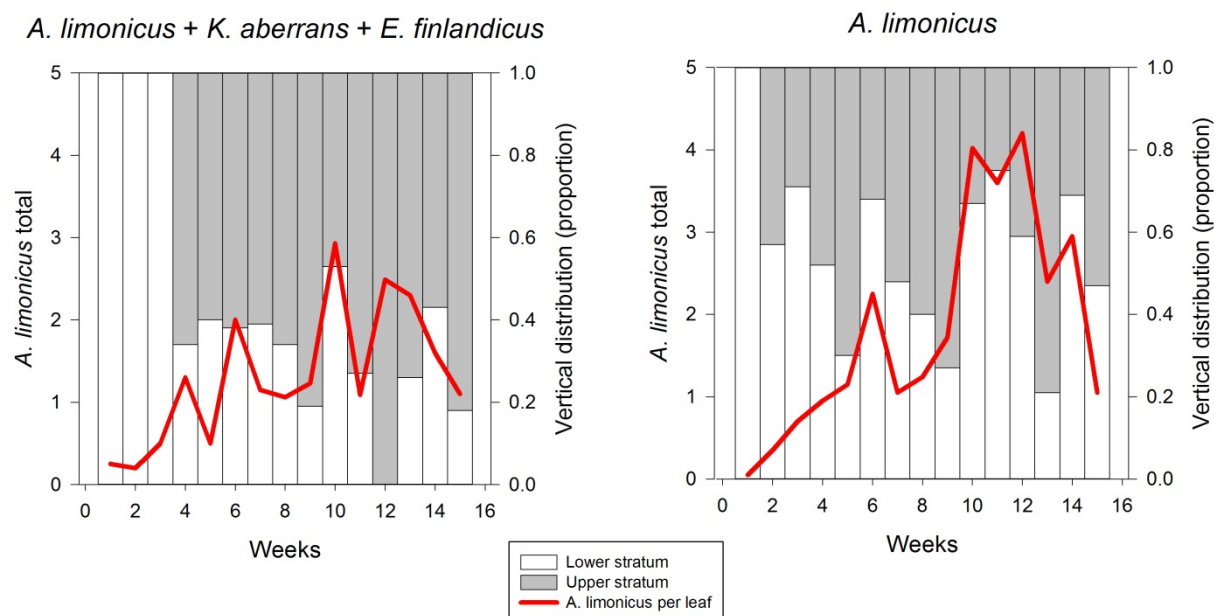
Figure 15. Population development and vertical distribution of alien *A. limonicus* in a two species system (*A. limonicus + K. aberrans + E. finlandicus*) and a single species system (*A. limonicus*) over 15 weeks.

**WP5**

The distribution map at present climatic conditions indicated that the European and African Mediterranean coast represents climatic conditions allowing the establishment of *A. limonicus*. However, the most suitable areas should be the Atlantic coast in Portugal and Spain with EI values over 40 (Fig. 18).
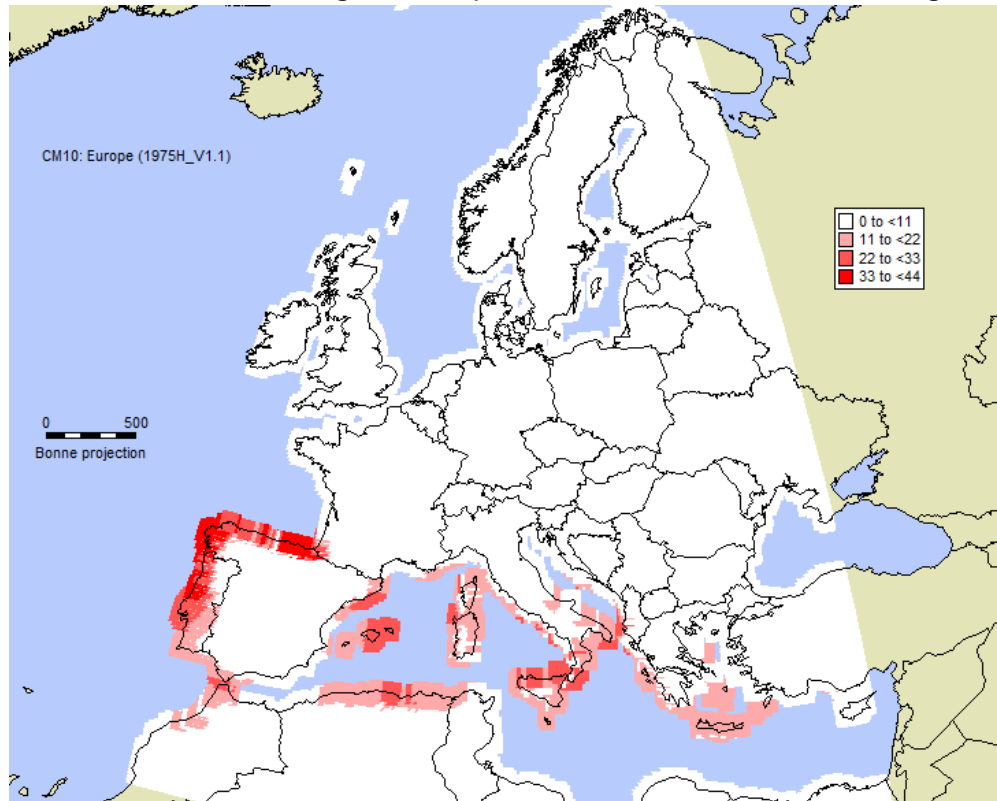


Fig. 16. Potential distribution of *A. limonicus* in Europe under present climatic conditions.

Climate warming should expand suitable areas for the establishment of *A. limonicus* in Europe with novel regions in the South of England and Ireland and along the Atlantic coast of France. According to the model calculations, the alien predator is not able to establish in Central Europe, including Austria (Fig. 17, 18).

Fig. 17. Potential distribution of *A. limonicus* in Europe under prospective climatic conditions using a RCP 4.5 scenario from 2020-2051 (upper figure) and 2071 to 2100 (lower figure) (reference period: 1981-2010).
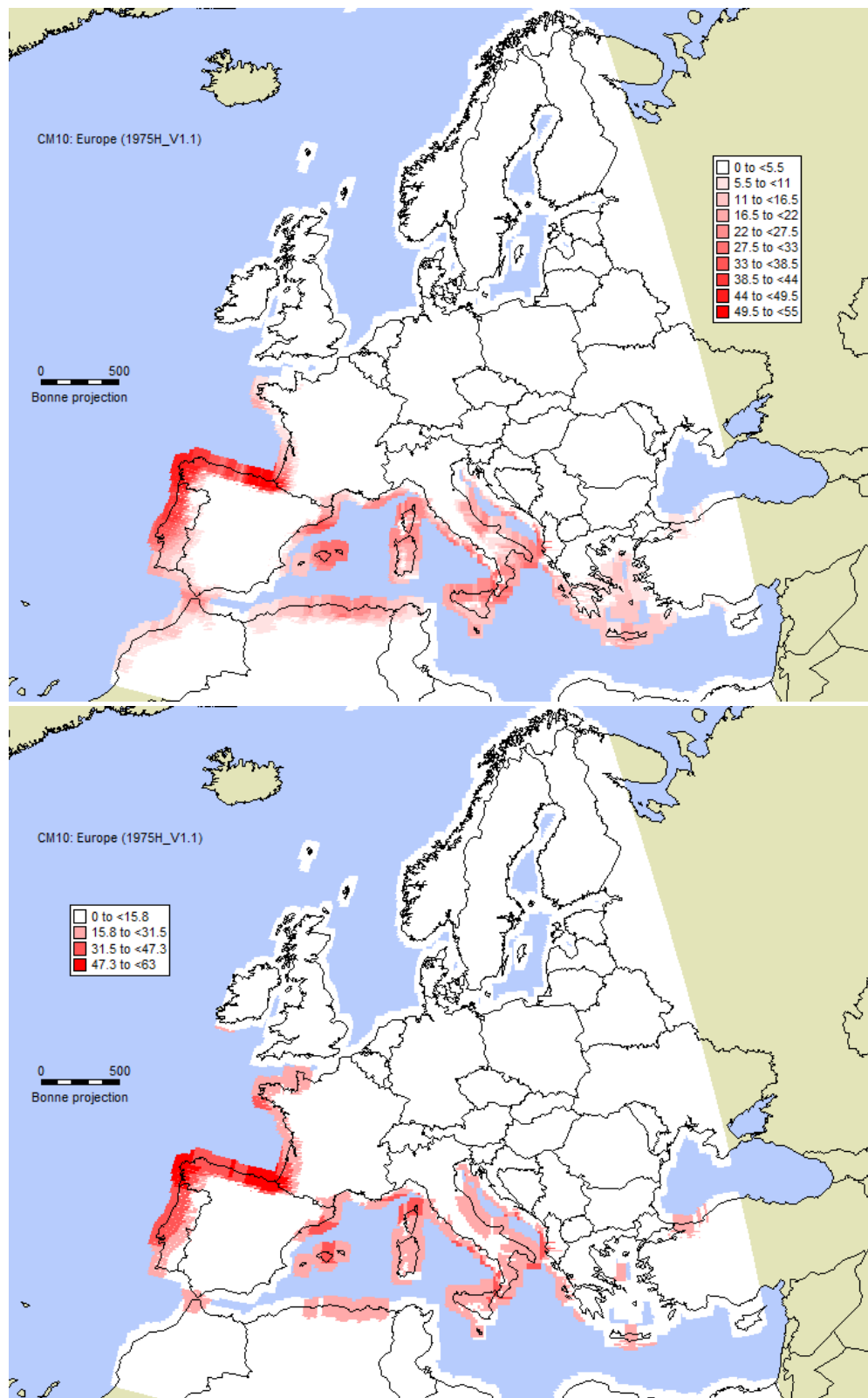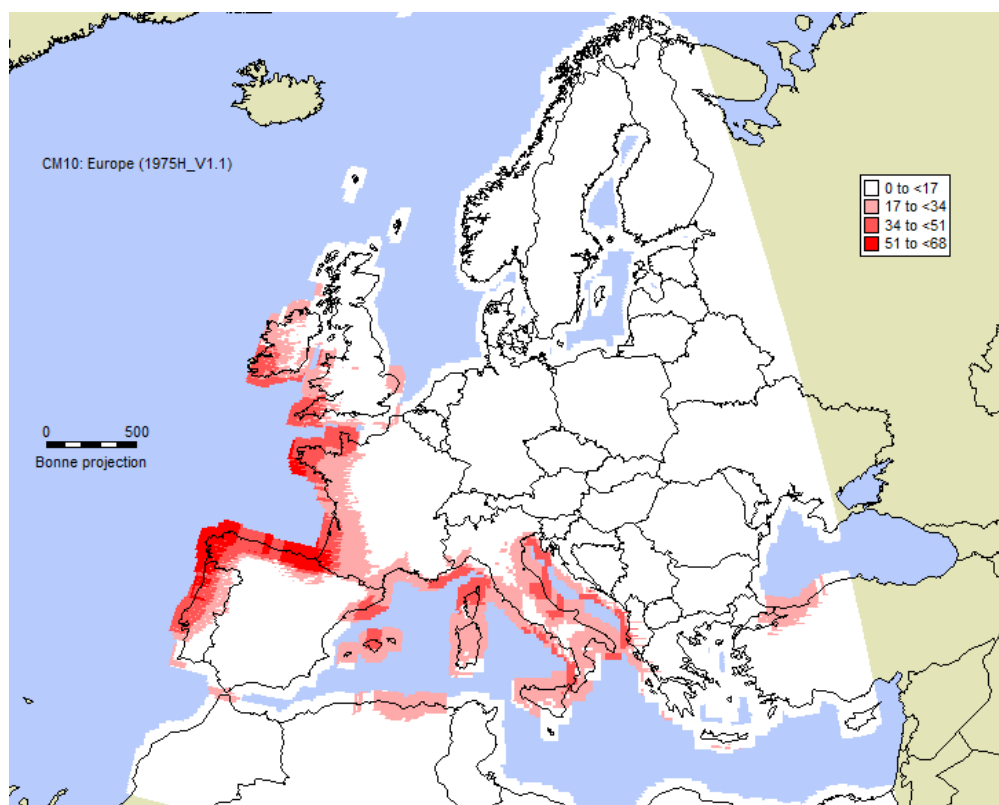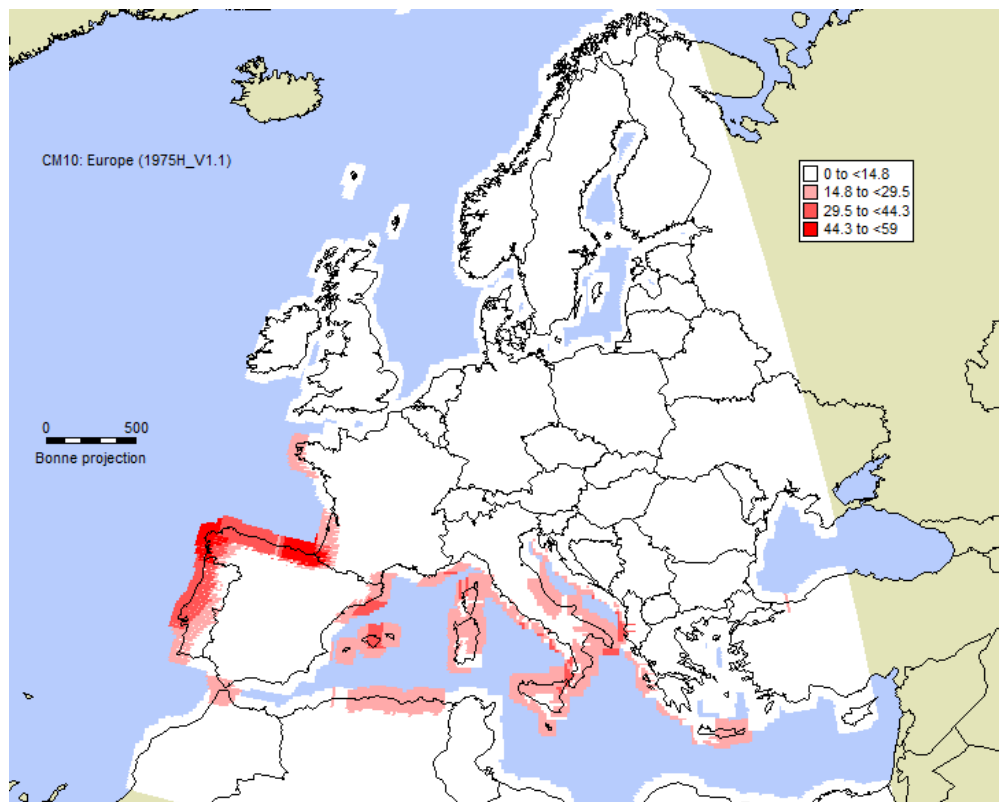
Fig. 18. Potential distribution of *A. limonicus* in Europe under prospective climatic conditions using a RCP 8.5 scenario from 2020-2051 (upper figure) and 2071 to 2100 (lower figure) (reference period: 1981-2010).

# 5 Conclusions and recommendations

**Abiotic resistance of native ecosystems to the alien predatory mite**

The ability to cope with winter temperatures in temperate regions is the pivotal determinant for the time-related establishment potential of alien species in Austria. Our results indicated that population development of *A. limonicus* is ensured within a temperature range of 10°C to 30°C with a thermal optimum around 27°C, characterizing this species as a heat-sensitive, but relatively cold-tolerant phytoseiid mite species that is not able to enter diapause. Acclimatization increased the cold-tolerance of *A. limonicus* females allowing the survival up to 6 weeks at permanent 0°C and 12 weeks at permanent +5°C. Furthermore, acclimatized females survived under field conditions cold waves up to $T_{min}$ values of -5°C, but not below this value. Native predatory mite females enter diapause at the beginning of winter induced by short-day conditions and decreasing temperatures, which drastically reduce their sensitivity to cold stress and ensure their survival during winter. Consequently, abiotic resistance of Austrian ecosystems should be high enough prevent regular overwintering and permanent establishment of *A. limonicus* both under present and prospective climate conditions because of its lack entering diapause. Also casual annual establishment of *A. limonicus* is also not very likely under present climate conditions. Not a single female survived the last two winters in the field, although the mean temperatures were relatively high (2016/17: +0.37°C; 2017/18: +2.17°C). Cold waves with $t_{min}$ values around -10°C occurred in both winter periods, which appear regularly each winter since 80 years in Eastern Austria as indicated by climatic records from Vienna and Lower Austria. Climate warming, however, lowers the abiotic resistance by the more frequent incidence of mild winters with a low number of frost days ($T_{min} < 0°C$), which in turn increases the casual annual establishment possibilities of *A. limonicus*. Independent of climate warming, establishment of *A. limonicus* is likely during the growing season in the case of escaping from greenhouses. The decreasing survival probabilities and egg production at permanent temperatures above 25°C and the impossibility of juvenile and female survival at 35°C characterize *A. limonicus* as heat-sensitive species. At a first glance, one may assume that the alien predator is not able to survive hot summer periods in Austria. However, the alien predator is well established in a predatory mite community in north-eastern Spain, where *A. limonicus* is often exposed to ambient $T_{max}$ values of 40°C in summer. Second, the majority of juveniles reached adulthood, when exposed to daily fluctuating temperatures with $T_{max}$ of 35°C. Consequently, it is assumed that increased summer temperatures caused by climate warming will not dramatically lower the seasonal establishment potential of *A. limonicus* in Austria.

## Population-specific trait differentiation

The cold-tolerance of *A. limonicus* seemed to be a conserved species-specific trait, because population differences were negligible. Thus, the potential establishment probabilities of *A. limonicus* during winter in Austria are not dependent on the population affiliation. In contrast, the performance of *A. limonicus* at moderate and high temperatures revealed population-specific responses resulting in considerable higher egg production of the SP population. Second, the alien SP population is well established in north-eastern Spain since 2011, where it competes for food with other native predatory mites. Thus, specimens of the SP population may possess or have evolved traits making them highly competitive against other competitors. Consequently, the SP population has better requirements to become established in Austrian predatory mite communities compared to the other populations. This population was also used in all further experiments.

## Inter-generational plasticity effects induced by heat stress

The offspring survival probabilities were very high (80 to 100%) and not affected by the thermal conditions of the offspring. These results clearly indicated that survival under natural conditions (daily fluctuating temperatures) is possible for *A. limonicus* also at high $T_{max}$ values in contrast to the exposure to constant high temperatures.

The thermal conditions of the *A. limonicus* parents clearly influenced the phenotypes of the next generation, which were dependent on the trait and offspring sex. Independent of the offspring environment, daughters and sons reached earlier adulthood deriving from parents reared under heat wave conditions. Size at maturity of sons was affected by the offspring environment, but not parental environment. They were smaller at heat wave conditions. The adult size of daughters, however, was larger, when the offspring environment matched the parental environment. Consequently, daughters gained a two-fold benefit, when deriving from parents reared under heat wave conditions. They are larger when reared under heat waves, which is an inter-generational plastic response induced by the offspring environment. Additionally, daughters, but also sons, reached earlier adulthood when deriving from parents reared under heat wave conditions.  This inter-generational effect, however, was independent on the offspring environment, which does not represent a plastic effect. Such inter-generational effects are termed "silver-spoon effects" or carry-over effects", where parents enable their offspring a heat start in life, irrespective of offspring environment. Both large body size and reaching early adulthood are assumed to have adaptive values for individuals exposed to heat waves. First, large individuals have lower transpiration loss and higher heat tolerance. Second, juveniles are more sensitive to heat stress than adults. Thus, reaching earlier adulthood reduces the time slot exposed to heat stress. These findings may indicate that inter-generational plasticity effects have the evolutionary potential allowing the alien predator to buffer and tolerate extreme climatic conditions such as heat waves.

### Biotic resistance of native predatory mite communities to the alien predator

Our findings clearly confirmed our hypothesis that the alien predator *A. limonicus* is superior in population growth and IG aggressiveness over native species, which should lower the biotic resistance of native predatory mite communities. However, climate warming may increase the biotic resistance of native predatory mite communities, because high temperatures lowered the IGP performance of *A. limonicus* against both native IG prey species but increased the aggressiveness of both native IG predator species against the *A. limonicus*. Thus, heat stress attenuated the IGP risk posed by *A. limonicus* and increased the vulnerability of *A. limonicus* as IG prey. Additionally, the native species *K. aberrans* reacted on the presence of the alien predator by antipredator responses. Naïve females (no experience with the predator) avoided egg deposition in prey patches containing alien predator traces and eggs, whereas experienced females counterattacked by killing eggs of the alien predator. Such antipredator responses against the alien predator also increase the biotic resistance of the native predatory mite communities.

### Establishment potential of A. limonicus in the field

*Amblydromalus limonicus* was not able to become dominant over the native species, but was able to establish and co-exist on apple saplings occupied by the native species *E. finlandicus* and *K. aberrans* over 15 weeks. More surprisingly, the native species *K. aberrans* was not affected by the presence of the alien predator. Four explanations may be put forward to explain these findings: (1) The dense hairiness of the apple leaves hindered the movement of fast running predators such as *A. limonicus*; (2) *A. limonicus*, but not *K. aberrans*, avoided leaves infested by high numbers of spider mites; (3) high temperatures in summer negatively affected the performance of the alien predator; (4) *K. aberrans* responded to alien predator cues by (a) avoiding leaves with *A. limonicus*, (b) executing counterattacks (IGP) or (c) searching for shelters. For example, rows of dense hairiness along both sites of the leaf midribs created a hollow space and *K. aberrans* females and their offspring, but not the other predators, were frequently found in this shelter. The population densities of the native *E. finlandicus* were lower in the presence of the alien predator *A. limonicus*. This species is a large, fast running and aggressive predator with a similar life style as *A. limonicus* making encounters between them more likely than between *A. limonicus* and *K. aberrans*. Thus, direct consumption effects of *A. limonicus* on *E. finlandicus* probably reduced their population densities. Nonetheless, *A. limonicus* females were able to compensate for the later settlement and asserted themselves on apple saplings despite the priority benefits of the native species.

### Modelling the invasion scenarios of A. limonicus in Europe under climate change

The areas, identified as suitable for the establishment of *A. limonicus* under present climatic conditions, nicely corresponded with the distribution pattern of *A. limonicus* at its native range. For example, *A. limonicus* is only found along the shore in California, but not in the dry inland. Similarly, the Mediterranean coasts, but not the inland, were identified to be suitable areas for the establishment of *A. limonicus*. Consequently, the application of the alien predator *A. limonicus* as biocontrol agent in Mediterranean countries poses a high risk of the permanent establishment, because these regions were identified as suitable for *A. limonicus*. Although the model estimations indicated an increase of the appropriate regions for invasion of *A. limonicus* because of climate warming, regions in Central Europe, including Austria, were not identified as suitable for *A. limonicus* establishment. Obviously, the winter conditions prevent the permanent establishment of *A. limonicus* in Austria.

### Summary

The alien predator *A. limonicus* should pose a low invasion risk for Austrian predatory mite communities irrespective of climate warming, because the alien predator is not able to establish permanently in Austria due to the lack entering diapause.  Additionally, also permanent establishment of the alien predator in a novel region (north-eastern Spain since 2011) had no negative effects on the native predatory mite community. Both abiotic (hot, dry summers) and biotic factors (high predatory mite diversity, antipredator responses of the native species) may be responsible for these findings that the alien predator co-exists with, but is not dominant over the native species since 7 years.  Along the same line, seasonal establishment on apple saplings occupied by two native Austrian species did not result in the elimination of native species. Nonetheless, a casual annual overwintering of *A. limonicus* in a mild winter caused by climate warming should create a priority benefit for the alien predator because of its earlier arrival on plants. If *A. limonicus* is able to be dominant over native species in such a scenario, remains an open question.

### Recommendations

The outcome of the project provided answers in relation to the formulated hypotheses, but there are still novel open questions. For example, when is a casual annual establishment of *A. limonicus* expectable because of climate warming? The application of an overwintering model, developed in the course of another ACRP-project (B060350: Predicting overwintering survival and establishment of alien pest insects under future Austrian climatic conditions), may be an appropriate way to estimate the casual winter survival probabilities of *A. limonicus* in Austria. Additionally, the survival probabilities of *A. limonicus* under natural conditions should be further observed in the next winter periods, in

order to detect a potential casual annual establishment as early as possible. Second, priority effects (the order in which species arrive into a community) are considered to be decisive for the establishment and invasion success of alien species. Plant community experiments revealed that species are rather dominant when arriving early, but alien species have lower costs when arriving late compared to native species. Seasonal establishment of *A. limonicus* means, that the alien predator escapes from greenhouses and arrives later on plants occupied by native predatory mite species. In the community experiment the alien predator was not dominant, when arriving later. However, the outcome of the interactions between native predatory mites and the alien predator strongly depends on the specificity of the tri-trophic system. For example, the establishment of *A. limonicus* should be favoured on plants with glabrous leaves, which may result in the elimination of native species. In the case of casual annual establishment the cold tolerant alien predator is probably arriving earlier than native species, which are in diapause until the end of April. The dominance of the alien predator over native species could be possible under these conditions. Thus, it is strongly recommended to (1) continue investigations on the future winter survival probabilities of *A. limonicus* and (2) evaluate the priority effects (the order in which species arrive into a community) on the establishment and invasion success of *A. limonicus* in Austrian predatory mite communities.

Finally, alien species comprise about a third of the authorized natural enemies (insects and mites) in Austria. These species might be sleepers activated by climate warming resulting in the shift from a beneficial to a pest species. Additionally, the number of applications for the authorization of alien biocontrol agents is probably increasing in the next years because of the increasing number of alien pest species. The Austrian registration authority AGES is probably forced to re-evaluate the effects of climate warming on the invasion potential of already authorized alien biocontrol agents and consider climate warming effects in its decision making for prospective authorization by the risk/benefit analysis of alien biocontrol agents. This research project may serve as a guideline to evaluate the establishment risk of alien arthropods.

# C) Projektdetails

## 6 Material and methods

All predatory mites used in the research project were fed with the two spotted spider mite *Tetranychus urticae* (Acari: Tetranychidae) and with pollen from narrow-leaved cattail *Typha angustifolia* (Nutrimite, Biobest, Belgium). The following three populations of the predatory mite *Amblydromalus limonicus* were evaluated in WP2 regarding their establishment potential in Austria: from the commercial producer Koppert (KO), an alien population from Spain (SP), and a native population from New Zealand (NZ). The abbreviations are used throughout WP2. SPSS 21.0.1 was used for all statistical analyses.
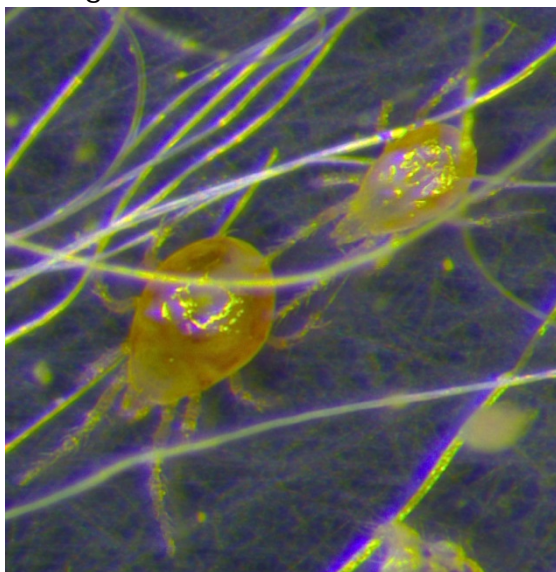


Fig. 1. *Amblydromalus limonicus* individuals (left: a larger female; right: a male).

**1. General rearing methods and experimental units**

The predatory mites were reared on detached bean leaves (native species *Euseius finlandicus*, *Kampimodromus aberrans*) or on plastic tiles (alien species *Amblydromalus limonicus*) placed on water-saturated foam cubes in plastic boxes half-filled with water. They were provided with pollen and spider mites (*A. limonicus*: alive spider mites; *E. finlandicus*, *K. aberrans*: frozen spider mites) in regular time intervals. Back-up rearing units were also established for all species/populations.

To obtain similarly aged eggs or adult females for the experiments, gravid females were collected from rearing units and placed on detached bean leaves in cohorts of 30 females provided with pollen and spider mites. After 8h the females were removed and the eggs (±4h old) or 10 days later the gravid females were used in the experiments. All these rearing units were placed in climate cabinets under constant environmental conditions (25°C, 16/8 L/D, 60 ± 5% RH).
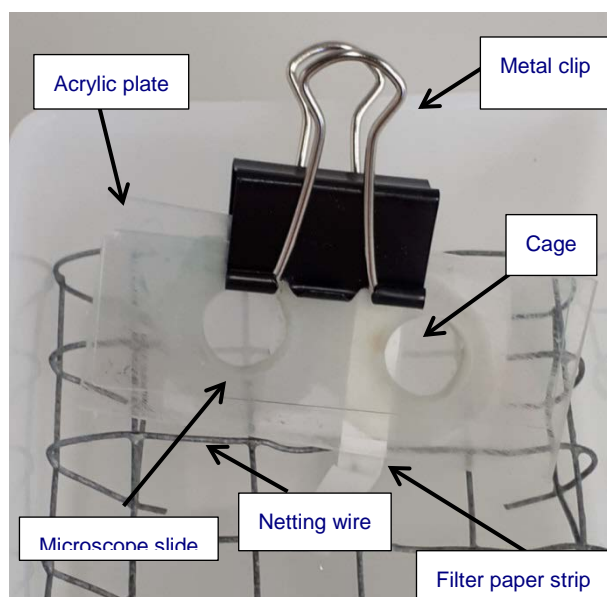
Fig. 2. A closeable cage placed in a plastic box half-filled with water.

Closeable cages were used as experimental units in the experiments 1.1.5.1.4 (WP1), 1.1.5.2.1, 1.1.5.2.2, 1.1.5.2.3, 1.1.5.2.4, 1.1.5.2.5, 1.1.5.2.6 (WP2), and 1.1.5.3.2 (WP3). They consisted of acrylic plates with two 15 mm diameter holes, which were the habitable room for the mites. Each hole was closed with a fine mesh screen at the bottom, which provided mites with adequate ventilation. The other side of the cage was covered with a microscope slide secured by a metal clip. The cages were placed on netting wire in a box half-filled with water. Water supply of the mites was provided by a filter paper strip, which was fixed at the bottom of the cage and had a connection to the water (Fig. 2).

In the no-choice experiments 1.1.5.3.3 (WP3), plastic tiles were used as experimental units, which were placed on water-saturated foams in plastic boxes half-filled with water. Water-saturated cellulose strips (5 mm height) at the margins of the tiles confined the arena. A barrier of fruit tree grease along the margins of the arena hindered the mites from escaping. Cotton wool strands under a cover glass served as shelter for the mites (Fig. 3).
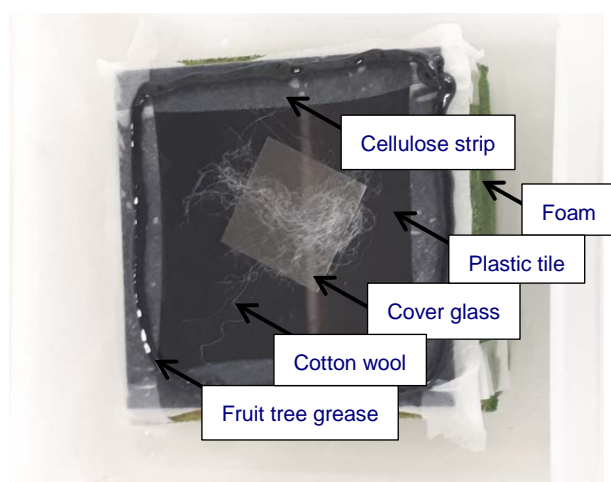


Fig. 3. Plastic tile arena placed in a plastic box half-filled with water.

In the choice experiments 1.1.5.3.3 (WP3) single bean leaves were used as experimental units. Two similarly sized leaflets (10-12 cm²), taken from trifoliate bean leaves, were placed upside down on the same foam cube in a plastic box (100 x 200 x 60 mm), half-filled with water, and were connected via a wax bridge (10 x 15 mm) (Fig. 4).
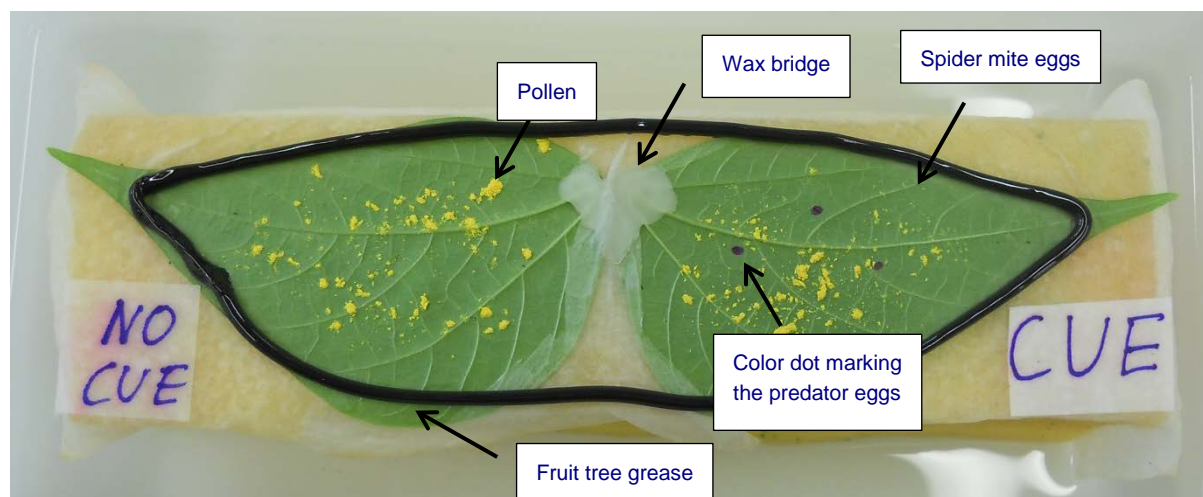


Fig. 4. Two bean leaflets (no cue: pollen + spider mite eggs; cue: pollen + spider mite eggs, IG predator traces + eggs), connected by a wax bridge on water–saturated foam placed in a plastic box, half-filled with water.

In the experiment 1.1.5.4 (WP4), organic apple saplings (*Malus domestica* M 9 BIO, 120 cm height, Silva Nortica, Bad Großpertholz, Austria), placed in plastic pots (Ø 27 cm), were used as experimental units, which were placed in mite-proofed wooden cages with a size of 60 x 60 x 140 cm closed with fine gauze (mesh opening: 109 µm) on every side. The gauze on the front side was closed by clips. Every experimental unit contained one apple tree in a pot (Fig. 5). Before the experiment was conducted the trees were kept for three months in a walk-in climate chamber at 25 ± 1°C, 60 ± 10%RH and 16:8 h L:D and were fertilized once with blue fertilizer (approx. 12% nitrogen, 12% phosphate, 17% potassium, 2% magnesium) to promote leaf growth. Due to an infection with aphids they were treated twice (23rd and 30th of May 2016) with a solution containing 2% of green soap (Neudosan Blattlausfrei, Neudorff GmbH, Emmerthal, Germany). On the 30th of June 2016 the trees were put into the experimental units located in the southeast of Vienna, Austria. In one of the experimental units a data logger (testo 177-H1 logger, Testo AG, Lenzkirch, Austria) was installed, that recorded the local temperature and humidity every hour. Before and during the experiments the trees were watered two to three times a week.

Fig. 5. Apple saplings in mite-proofed cages at the premises of the company biohelp.

## 2. Experimental set-up for each experiment

### WP1

1.1.5.1.4: IG Aggressiveness between the alien predator *Amblydromalus limonicus* and its native counterpart *Amblyseius andersoni*

A single IG predator (female) and single IG prey (larva) were placed in a closeable cage (*A. limonicus* as predator and *A. andersoni* as prey and vice versa) and the time elapsed until the first attack occurred was evaluated each 10 min in the lab (25°C, 60 ± 5% RH) over 360 min. All statistical analyses were conducted using SPSS 21. The attack functions of the IG predator species (combination of cumulative attack proportion and attack time) were compared by using Kaplan-Meier analyses. Generalized linear models (GLMs) were used to analyze the IG predator effects on predator and prey activity, IGP success (prey killed or not) and IG prey survival (yes/no) (binomial distribution, logit link function). GLM's were also used to compare the IG predator and IG prey effects on body size.

### WP2

1.1.5.2.1: Temperature effects on reproduction and development

The developmental progress of single eggs (± 4h) in closeable cages was observed twice per day, when exposed to a temperature gradient from constant +10°C to 35°C in 5°C steps. The experiments were finished, when the juveniles reached adulthood or died. Then the adults were mounted on microscope slides using Hoyer's medium and the sex and body size (perimeter of the dorsal shield) were determined. Second, gravid and similarly aged females, placed singly in closed cages, were observed over 10 days and the number of deposited eggs was recorded every 24h. Both juveniles and females were provided with water,

spider mites and pollen during the experiments. The temperature (+10°C, +15°C, +20°C, +25°C, +30°C, +35°C), population (KO, SP, NZ) and sex (female, male) effects on age and size at maturity (normal distribution, identity link function) were analyzed by using generalized linear models (GLM's). To detail sex-specific temperature effects on age and size at maturity within and between the populations, pairs of the estimated marginal means were compared by least significant difference (LSD) tests. Similarly, GLM's were used to compare the temperature and population effects on juvenile and adult survival (binomial distribution, logit link function) and fecundity (normal distribution, identity link function). To detail temperature effects on survival and fecundity within and between the populations, pairs of the estimated marginal means were compared by least significant difference (LSD) tests.

## 1.1.5.2.2: Diapause induction

Cohorts of eggs from egg rearing arenas of each *A. limonicus* population and of *E. finlandicus* were put on detached bean leaves placed on water saturated foam cubes in plastic boxes, half-filled with water. The predatory mite eggs were provided with water, pollen of and spider mites and exposed to short day conditions (18 ± 1°C; 8:16 L:D). After 10 days all juveniles reached adulthood and then gravid *A. limonicus* and *E. finlandicus* females were singly placed in closed cages together with a conspecific male for 20 days under short day conditions (18 ± 1°C; 8:16 L:D) and provided with water, pollen and spider mites. Males were replaced by other males every 5 days. After 20 days only non-ovipositing females were exposed to long day conditions (25 ± 1°C; 16:8 L:D) for another 10 days. The criterion for diapause induction was the absence of egg production at short day conditions and subsequent resuming of egg production at long day conditions.

## 1.1.5.2.3 + 1.1.5.2.4: Lower lethal time (cold tolerance) and thermal tolerance plasticity

Single, young, non-acclimatized (reared at 25°C) and acclimatized (reared 4 weeks at 20°C, then 4 weeks at 15°C) *A. limonicus* females were placed in closed acrylic cages with water supply and were exposed to temperatures of -5°C, 0°C, 5°C and 15°C . At 5°C and 15°C the females were additionally provided with pollen and spider mites. The state of the females (dead, alive) was recorded every 3 and 7 day per week over a period of 12 weeks (winter duration in Austria). Eggs deposited at +5°C and +15°C were reared at +15°C to evaluate the larval hatchability. The survival functions of the females (combination of cumulative survival proportion and survival time) were analyzed by using Kaplan-Meier analyses with pairwise Breslow tests. The temperature and acclimatization effects on the egg number (normal distribution, identity link function) and their hatchability (binomial distribution, logit link function) were analyzed by GLM's. To detail acclimatization effects on egg number and hatchability within and between the temperatures, pairs of the estimated marginal means were compared by least significant difference (LSD) tests.

1.1.5.2.5: Winter survival under natural thermal conditions

An additional semi-field experiment was conducted to evaluate the survival probabilities of *A. limonicus* under natural winter conditions in 2016/17 and 2017/18. The cold-acclimatized females (reared 4 weeks at 15°C, then 4 weeks at 10°C) were placed singly in closable cages provided with water, pollen and spider mites. Females of the native *E. finlandicus* were used as control species. The cages were placed in small, open boxes sited in the ground vegetation layer of apple saplings grown in pots at the premises of the company biohelp. The boxes were placed under a wooden roof to protect the cages from rain. Both ambient temperature and the temperature in the ground vegetation layer were recorded during the experiment by using data loggers (HOBO UX100-001). The evaluation of the state of the mites (dead, alive) was conducted weekly from the beginning of December 2016 and 2017 until all *A. limonicus* females died. The survival functions of the females (combination of cumulative survival proportion and survival time) were compared between *A. limonicus* and *E. finlandicus* by using Kaplan-Meier analyses.

1.1.5.2.6: Intra- and trans-generational effects on age and size at maturity induced by heat waves

To evaluate intra-generational effects on age and size at maturity, similarly aged eggs (±4h) from the egg rearing units were placed in closeable cages and were exposed to common summer conditions (daily $T_{max}$: 30°C, $T_{min}$: 15°C, $T_{mean}$: 22.9°C) or heat wave conditions (daily $T_{max}$: 35°C, $T_{min}$: 18°C, $T_{mean}$: 24.8°C). The juveniles were provided with water, spider mites and pollen. The developmental progress was evaluated twice per day until the juveniles died or reached adulthood. Then the adults were mounted on microscope slides using Hoyer's medium and the sex and body size (perimeter of the dorsal shield) were determined. To obtain eggs for the offspring generation, similarly aged eggs (±4h) from the egg rearing units were reared under common summer conditions or heat wave conditions until the juveniles reached adulthood and mated. Then the gravid females were placed in closeable cages for egg production within 8h. These eggs were then used for the evaluation of trans-generational effects on age and size at maturity induced by heat waves in an identical manner as in the intra-generational effects experiments. The intra-generational plasticity effects induced by heat waves were analyzed by comparing the survival of the parental generation exposed to common summer conditions or heat wave conditions using GLM's (binomial distribution, logit link function). Sex (male, female) was added as additional factor for the intra-generational plasticity effects on age and size at maturity (normal distribution, identity link function) of the parental generation. To detail the intra-generational effects within and between males and females, pairs of the estimated marginal means were compared by least significant difference (LSD) tests. The effects of parental environment (common summer conditions, heat wave conditions) and offspring environment (common summer conditions, heat wave conditions) on juvenile survival of the offspring generation were analyzed using GLM's (binomial distribution, logit link function). The effects of parental and offspring environment on age and size at maturity were analyzed

separately for males and females. To detail the inter-generational effects within and between parental and offspring environments, pairs of the estimated marginal means were compared by least significant difference (LSD) tests.

**WP3**

1.1.5.3.1: Capacity for population increase

Data on juvenile survival and development, adult survival, oviposition and offspring sex ratio generated by the life history experiments were used to calculate the intrinsic rates of increase ($r_m$) per population and temperature by Jackknife estimates using the program based on SAS 9.1. The pairwise comparisons of the $r_m$-values among the *A. limonicus* populations within each temperature were conducted with two-tailed t-tests for independent samples using LIFETABLE.SAS.

1.1.5.3.2: Categorization of native and alien IG prey and predators

Single females of the three species *E. finlandicus*, *K. aberrans* (native species) and *A. limonicus* (alien species) were placed in closed cages as IG predators and provided with single IG prey larvae in all possible combinations at 26°C, 29°C and 32°C. The time elapsed until an attack occurred were recorded every 5 to 10 min during 6h. The attack functions of the IG predator species (combination of cumulative attack proportion and attack time) were compared by using Kaplan-Meier analyses with pairwise Breslow tests.

1.1.5.3.3: Learning effects on the interaction between native IG prey and alien predator

In the no-choice experiments a single gravid predator (*A. limonicus* or *K. aberrans*) was placed on a plastic tile (Fig. 3) and provided with 15 larvae and 10 protonymphs as IG prey, which was replenished each day. The number of killed IG prey and the deposited eggs by the predator females were evaluated every 24h over three days. To generate naïve and experienced IG predators (females) and prey (larvae), *A. limonicus* and *K. aberrans* females were reared alone or together on bean leaves. The learning effects of IG predators (prey-experienced, prey-naïve) and prey (predator-experienced, predator-naïve) on IG predation and egg production were analyzed separately for each species (alien species *A. limonicus*, native species *K. aberrans*) by using GLM's (normal distribution, identity link function).     In the choice experiment, one leaflet only harbored spider mite eggs and pollen and the other spider mite eggs, pollen and IG predator cues (Fig. 4). The wax bridge was blocked by a moist filter paper during the preparation of the choice units. 48h before experimental start, 10 *T. urticae* females were placed on each leaflet allowing oviposition for 24 h. Then the spider mites were removed and two IG predator females were placed on one of the two leaflets allowing consumption of pollen and spider mite eggs for 24h. Then the predators were removed and the number of spider mite eggs was adjusted to 40 per arena in both leaflets and the predator egg number to 4 eggs in the arenas with the IG predator cues. The position of the IG predator eggs was marked by a tiny watercolor dot on the leaf surface to ease the evaluation of potential IG

predation of the experimental mothers. In that manner we created two prey patches with identical spider mite densities (40 eggs) and pollen (standardized amount), but one prey patch also harbored IG predator cues (Fig. 3). Then the filter paper was removed from the wax bridge and the IG predator-experienced or predator-naïve mothers (gravid and similarly aged, identical hunger level) were placed in the middle of the wax bridge. The prey patch choice of the females was recorded after 24 and 48h. Additionally, the number of deposited eggs in each prey patch and the number of killed predator eggs in the prey patch with IG predator cues were also evaluated after 24 and 48h. The predator-naïve females were taken from the rearing units. To obtain predator-experienced females, the following set-up was used: two detached bean leaves, surrounded by fruit tree grease, were placed one after the other on water-saturated foams in a closeable plastic box, separated by a plastic wall with an open end. The box had two holes at the small sites, which were the input and output for the airflow. The input at the right site was connected with Plexiglas chamber with activated charcoal to purify the air sucked into the plastic box. The output at the left site was connected to an area flowmeter and a mini-diaphragm vacuum pump. The flow rate was adjusted to 2.5l min$^{-1}$ (Fig. 6).  Four IG predator females were placed on the leaflet at the right site of the box and provided with IG prey (10 eggs, 10 larvae). Cohorts of ten gravid females from the species used as IG prey were placed on the leaflet at the left site of the box and provided with water, pollen and spider mite eggs. Then the plastic box was closed and the vacuum pump was activated creating an airflow from the leaflet containing the IG predators and prey to the leaflet containing the gravid females used in the choice experiment. In that way the females were exposed to cues emitted from the IG predators and IG prey (alarm pheromones).
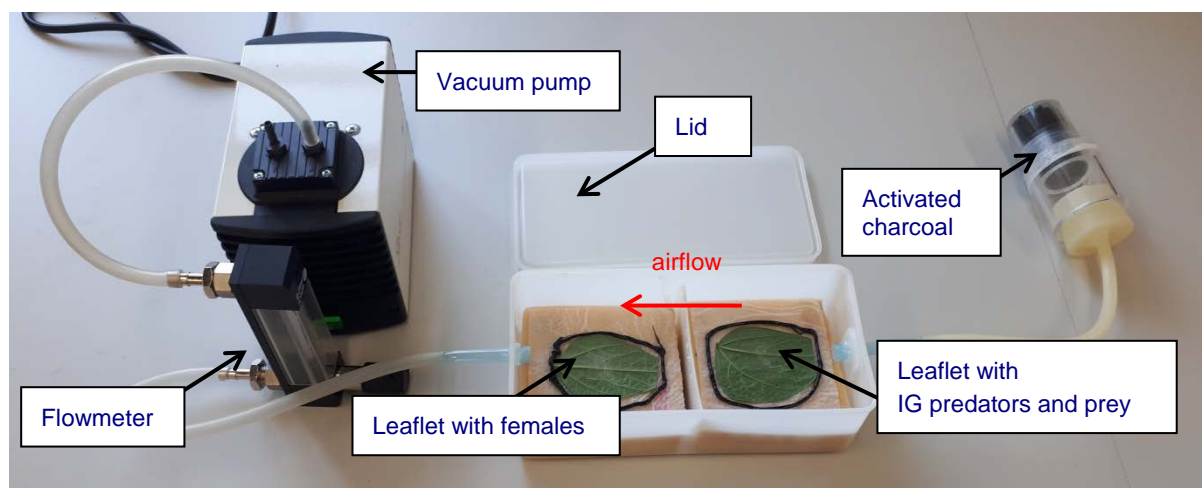


Fig. 6. Set- up for generating IG predator experienced females for the choice experiments.

**WP4**

1.1.5.4: Establishment potential of *A. limonicus* in the field

Three treatments (10 replicates per treatment) on apple saplings as experimental units were conducted: (1) a single-species system with the alien

predator *A. limonicus* alone, (2) a two-species system with the native species *K. aberrans* and *E. finlandicus*; and (3) a three-species system with the alien predator and the two native species. On 30th June 2016 four gravid females of the spider mite *T. urticae* and two gravid females of the Western Flower thrips *Frankliniella occidentalis* were released on the apple saplings. Additionally, pollen (0.25 g *T. angustifolia*) was applied on the trees each week. On 07th July four young, gravid *K. aberrans* and *E. finlandicus* females were placed on apple saplings per replicate. Then also four females of the alien predator *A. limonicus* were also introduced on the plants on 20th July. The plants were subdivided in two vertical strata: the lower stratum up to a height of 80 cm and the upper stratum above 80 cm. All developmental stages of the spider mites and predatory mites, thrips and the availability of pollen (present/absent) were counted each week by sampling single leaves from each stratum. After mite counting the leaves were returned with the mites to the apple saplings by the fixation with clips on the branches.

Generalized estimated equations (GEE's) were used to analyze the effects of species composition and time on the population development of each predatory mite separately. To detail the species composition effects within and between the time points, pairs of the estimated marginal means were compared by least significant difference (LSD) tests.

**WP5**

Climex 4.0 (Hearne Scientific Software, Melbourne, Australia) was used to estimate the distribution of *Amblydromalus limonicus* under present and prospective climatic conditions. The software uses a hydro-thermal growth index to describe conditions that favour the growth of a population, in addition to four stress indices (cold, heat, dry, wet) and their interactions, which describe unfavourable effects of temperature and moisture. A combination of the growth and stress indexes leads to the ecoclimatic index (EI), ranging from 0 to 100. A species is not able to persist, when EI is 0, but an EI over 30 represents a favourable climate. The CliMond 10´ resolution climate data (download from https://www.climond.org/ClimateData.aspx) were used to represent the historical climate (1961-1990) in Climex 4.0. Data for the temperature values and degree-days per generation of *A. limonicus* Climex parameters for *A. limonicus* were used from our experiments (WP2). All other Climex parameters were manually and iteratively adjusted until the simulated suitability patterns estimated by the EI values most closely matched the known worldwide geographical distribution of *A. limonicus*. The parameter values are presented in table 1.

Table 1. Climex parameter values used to model the geographical distribution of *A. limonicus.*

| Variable | Parameter | Value |
|---|---|---|
| Temperature | Limiting low temperature | 10 |
| | Lower optimal temperature | 20 |
| | Upper optimal temperature | 27 |
| | Limiting high temperature | 30 |
| Moisture | Limiting low moisture | 0.25 |
| | Lower optimal moisture | 0.7 |
| | Upper optimal moisture | 1.5 |
| | Limiting high moisture | 2.5 |
| Cold stress | Temperature threshold (average) | 9 |
| | Temperature rate (average) | -0.002 |
| Heat stress | Temperature threshold (average) | 32 |
| | Temperature rate (average) | 0.005 |
| Dry stress | Dry stress threshold | 0.20 |
| | Dry stress rate | -0.005 |
| Wet stress | Wet stress threshold | 2.5 |
| | Wet stress rate | 0.002 |
| Hot-Dry stress | Hot-Dry stress threshold | 25 |
| | Hot-Dry moisture threshold | 0.1 |
| | Hot-Dry stress rate | 0.09 |
| Generation | Degree-days per generation | 100 |

Temperatures are in °C, moisture is the proportion of soil moisture holding capacity, rates are in week$^{-1}$, degree-day is the sum of °C x day$^{-1}$ above 10°C.

The scenarios are based on different radiative concentration paths of the greenhouse gases (RCP's), whereas RCP 4.5 and RCP 8.5 correspond to radiative forces of 4.5 Wm$^{-2}$ and 8.5 Wm$^{-2}$ respectively. The data for modelling were from the project CORDEX for the domain Europe in high resolution (EUR-11). The following two models were used: ICHEC-EC-EARTH_rcp4.5_KNMI-RACMO22E; and ICHEC-EC-EARTH_rcp8.5_KNMI-RACMO22E. The reference period was 1981-2010, and the periods for the projections were: 2021-2050 and 2017-2100. The parameter values are presented in table 2.

Table 2. Climate parameters used to model the distribution of *A. limonicus* under climate scenarios.

| Parameter | Scenario | | | |
|---|---|---|---|---|
| | RCP 4.5 | | RCP 8.5 | |
| | 2021-2050 | 2071-2100 | 2021-2050 | 2071-2100 |
| Min. Temp. Change (Winter)[1] | 0.83 | 1.91 | 1.18 | 3.68 |
| Min. Temp. Change (Summer)[1] | 1.61 | 1.89 | 1.34 | 3.58 |
| Max. Temp. Change (Winter)[1] | 0.79 | 1.81 | 1.08 | 3.54 |
| Max. Temp. Change (Summer)[1] | 1.04 | 1.69 | 1.21 | 3.31 |
| Rainfall change (Winter)[2] | 0.4 | 2.8 | 1.9 | 4.3 |
| Rainfall change (Summer)[2] | 0.4 | 3.3 | 1.16 | -4.18 |
| Evaporation change (Winter)[2] | 2.35 | 3.865 | 1.25 | 7.23 |
| Evaporation change (Summer)[2] | 2.55 | 3.2 | 2.1 | 5.945 |

[1]°C, [2]%

# 7 Work and time schedule

| | Months | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 1-6 | 7-12 | 13-18 | 19-24 | 25-30 | 31-36 | 37-42 | 43-46 |
| Literature review | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| Mite rearing | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| Pilot experiments | ■ | ■ | | | | | | |
| WP1 | | ■ | | | | | | |
| WP2 | | | ■ | ■ | | | | ■ |
| WP3 | | | | | | ■ | ■ | |
| WP4 | | | | ■ | ■ | | | |
| WP5 | | | | | | | | ■ |
| Statistical data analyses | | | ■ | ■ | ■ | ■ | ■ | ■ |
| Manuscript preparation | | | | ■ | ■ | ■ | ■ | ■ |
| Research presentation | | | | ■ | ■ | ■ | ■ | ■ |

# 8 Publications and other activities

**2015**

Published contribution and presentation for a scientific congress

Dittmann, L; Walzer, A; Schausberger, P (2015): Strain-specific cold tolerance of the predatory mite Amblydromalus limonicus.
[IOBC/WPRS, 5th Meeting of the IOBC Working Group "Integrated Control of Pest Mites", Castello de la Plana, SEPT 8-10, 2015]
In: IOBC/WPRS, 5th Meeting of the IOBC Working Group "Integrated Control of Pest Mites", http://iobcmites2015.es/

Walzer, A; Dittmann, L; Schausberger, P (2015): Comparing the potential of Amblydromalus limonicus strains to overcome abiotic resistance of Austrian ecosystems under climate warming scenarios.
[IOBC/WPRS, 5th Meeting of the IOBC Working Group "Integrated Control of Pest Mites", Castello de la Plana, SEPT 8-10, 2015]
In: IOBC/WPRS, 5th Meeting of the IOBC Working Group "Integrated Control of Pest Mites", http://iobcmites2015.es/

**2016**

Published contribution and presentation for a scientific congress

Dittmann, L; Walzer, A; Schausberger, P (2016): Thermal sensitivity of *Amblydromalus limonicus* regarding its establishment potential in Austria under climate warming.
[8th Symposium of the European Association of Acarologists, Valencia, Spain, July 11-15, 2016]
In: European Association of Acarologists, 8th Symposium of the European Association of Acarologists, p 48

Dittmann, L.; Walzer, A.; Schausberger, P. (2016): Einfluss der Klimaerwärmung auf das Etablierungs- und Invasionspotenzial eines exotischen Nützlings in Österreich: die thermale Sensitivität der Raubmilbe *Amblydromalus limonicus*.
[17. Klimatag. Aktuelle Klimaforschung in Österreich, Graz, 6-8. April]
In: Climate Change Centre Austria, Tagungsband 17. Klimatag

Escudero-Colomar, L-A; Creus-Peraferrer, E; Chorazy, A; Walzer, A; (2016): Intraguild predation between the native species Amblyseius andersoni and the alien species *Amblydromalus limonicus* (Acari: Phytoseiidae).
[9th International Conference on Integrated Fruit Production, Thessaloniki, GREECE, SEPT 4-8, 2016]
In: IOBC - WPRS, 9th International Conference on Integrated Fruit Production, Abstract book, p. 147

Walzer, A; Dittman, L; Schausberger, P (2016): Kann die exotische Raubmilbe *Amblydromalus limonicus*, ein Pflanzennützling, aufgrund der Auswirkungen des Klimawandels in Österreich überwintern? [Poster]
[17. Klimatag. Akuelle Klimaforschung in Österreich, Graz, 6-8. April]
In: Climate Change Centre Austria, Tagungsband 17. Klimatag

**2017**

Presentation for a scientific congress

Walzer, A; Dittmann, L; Schausberger, P (2017): Die thermale Sensitivität des exotischen Nützlings Amblydromalus limonicus.
72. ALVA-Tagung, "Zukunft Obstbau", MAY 22-23, 2017, Waldkirchen am Wesen

Walzer, A; Dittmann, L; Schausberger, P (2017): Temperature-dependent intraguild predation risk of native predatory mites by an alien predator.
IOBC Canada 2017, Integrated control in protected crops, temperate climate, JUN 4-8, 2017, Niagara Falls

Published contribution in a non-scientific journal
Walzer, A. (2017): Projektvorstellung, CAS newsletter, Centre of Agricultural Sciences, 02/2017.

Diese Projektbeschreibung wurde von der Fördernehmerin/dem Fördernehmer erstellt. Für die Richtigkeit, Vollständigkeit und Aktualität der Inhalte sowie die barrierefreie Gestaltung der Projektbeschreibung, übernimmt der Klima- und Energiefonds keine Haftung.

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