Alien insect species in a warmer world – patterns and trends

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Introduction

Climate change and biological invasions are key processes affecting biodiversity and ecosystem services (Sala *et al.* 2000). However, until now their effect on biodiversity has almost exclusively been targeted independently. Moreover, there are good scientific reasons to expect the rate and extent of biological invasions to increase under climate change (Simberloff 2000, Ward and Masters 2007). Hence, the various drivers of global change in general and climate change and biological invasions in particular, should be considered in a more integrated manner.

Mean global temperature has increased by ca. 1°C since the pre-industrial era with an acceleration during the last decades where 8 out of the 10 years between 1996 and 2007 were among the warmest ones since 1850 (EEA, 2008). Thus, climatic isotherms have moved northwards of 120 km on the average during the past century (Parmesan *et al.*, 1999). Taking into account different change in concentration of greenhouse gases, climate scenarios predict a further range of temperature increase of 1.6- 6.4°C by 2100 (IPCC, 2007). Simultaneous changes in rainfall regimes and in frequency of extreme climatic events are predicted. Because insect species are poikilotherm, they are likely to respond very quickly to temperature changes (Logan *et al*., 2003). Shifts in climatic conditions may affect survival, fecundity, development and dispersal, and signs of their response to global warming have already been detected in native insect species (Parmesan & Yohe, 2003; Battisti *et al.*, 2005; Parmesan, 2006). Similar to these observed ecological responses of native species to climate change, climate warming may directly influence the introduction and colonisation of alien insect species into new territories, it may affect their establishment rates and it may also facilitate the spread, and increase, or decrease the effect of alien species already present in the environment. Furthermore, an indirect effect of climate change may be realised as some native ecosystems may become less resistant to invasion under future climates, especially with regard to drought (see Rouault *et al.*, 2006).

In recent years, there has been an increasing number of reported case studies showing that a wide range of alien taxa introduced from warmer climes reproduce and establish in previously unsuitable areas and as a result enlarge their range of distribution. More than 400 insect species of Australasian, African and Central and South American origin appeared to have established in Europe, with most of them occurring in the Mediterranean region (Roques *et al.*, 2009). Such a climatically-triggered invasion process often starts with a few precursor individuals, which only temporarily occur in a site during short favourable climatic periods or, in this early stage, are spatially restricted to favourable micro-habitats. Continued climatic warming may prolong the duration of these occasional occurrences of initial introductions, increase their frequency or enlarge the range and area of suitable habitats; thus, making it more likely for these species to persist, to occur more frequently and to develop larger populations. With further global warming, alien species originating from warmer regions may build up both numerically and spatially larger populations that may spread to wider areas.

However, a major issue consists in understanding whether the observed changes can really be attributed to a variation in climatic conditions. It is usually difficult to entirely disentangle the effect of climate change from that of other physical or chemical factors, and/or other biotic causes, especially man-mediated changes in land use and habitat modifications (). Most studies have focused on the effects of temperature, but other climatic factors are probably important as well, e.g., isolation, relative humidity, rainfall, CO_2 concentration …, and that is their combination which really determines the weather conditions experienced by the individuals. For instance, the establishment of an invasive Asian mosquito, *Aedes albopictus* (Diptera: Culicidae), depends on temperature but also on photoperiod, humidity and rainfall (Eritja *et al*., 2005). Even though testing the effect of one factor in laboratory conditions is relatively easy, testing the effects of numerous factor combinations is extremely complex and some contradictory results may appear (see Newman, 2005). Moreover, climate change may affect not only insect populations but also their host plants, natural enemies, mutualists, and competitors (Ayres & Lombardero, 2000; Walther *et al*., 2002).

In this paper, we (1) synthesize the evidence for changes in insect biological invasions arising from recent climatic changes, (2) evaluate the relative importance of both the direct and indirect effects of climate change on insect invasions, (3) contrast these findings with studies on climate-induced changes of native insect species, and (4) try to identify trends for the future.

Global warming is offering new opportunities for introductions

Populations of alien insects are considered more likely to survive if they are introduced to areas with climatic conditions similar to those in their native distribution range. Temperature is a key factor affecting growth, survival and reproduction in both a direct and indirect way. Hence, the survival of alien species introduced from habitats in warmer regions to new areas with harsher conditions either depends on locally heated 'islands' or on changing climate in the introduced range. Urban areas act as warm islands in northern latitudes providing opportunities for e.g. thermophilous ants such as *Lasius neglectus* (Dekoninck *et al.*, 2002). Anthropogenic habitats, especially buildings, are also first habitats for spiders alien in or to Europe (Kobelt & Nentwig 2008). Similarly, Kiritani (2006) suggested greenhouses in temperate environments that host exotic pests of sub-tropical or tropical origin, as a model of outdoor temperate agro-ecosystems after global warming. Indeed, about 66% of the exotic insect species established in Europe are only found in anthropogenic habitats at this moment (Roques *et al.*, 2009).

Global warming could provide new opportunities for introductions to areas where, until recently, introduced species were not able to survive. Former greenhouse inhabitants, such as three exotic scale species, *Diaspidiotus distinctus*, *Coccus hesperidum* and *Icerya purchasi*, have recently been found outdoors in Switzerland (Kenis, 2006). Also non-native biological control agents of greenhouse pests start to establish outside the greenhouse environment, such as the predatory bug *Macrolophus caliginosus* (Hart *et al.* 2002) and the predatory mite *Neoseiulus californicus* (Hatherly *et al.* 2005) in the UK. Similarly, pine processionnary moth, *Thaumetopoea pityocampa*, has recently been accidentely introduced with large potted pine trees in the Alsace region of France, i.e., 180 km far beyond its natural range. Whilst the climatic conditions did not allow larvae to survive during the 1990s because of winter temperatures under the survival thresholds, the warming up of the area since 2000 resulted in the establishment of self- sustaining moth populations.

In addition to the removal of physiological constraints, climate change may also open up unprecedented introduction pathways. The long-range dissemination of organisms by air is to a major degree controlled by atmospheric circulation patterns and often depends on extreme climatic events (Greenslade *et al.* 1999). Insects may profit, because of their small size, from ocean and air currents or migration of hosts/vectors to colonise new ecological areas. The recent arrival of the migratory moth *Plutella xylostella*, a cosmopolitan vegetable pest, into Svalbard Island (High Arctic - Norway) was due to an unusual air mass that crossed from West Russia (Coulson *et al.* 2002). Increased temperatures may also prolongate the flying period of insects and thereby enable them to become dispersed over greater distances (Ott 2009). For instance, migration patterns of the silver Y moth, *Autographa gamma* (Lepidoptera: Noctuidae), to Britain are largely influenced by the changes in temperatures and rainfall in its overwintering sites of North Africa (Chapman *et al.*, 2008). Using classical climate change scenarios, Harrington *et al.* (2007) also calculated that the first aphid occurrence is expected to occur, on average, one day earlier every four years in Europe.

Global warming may facilitate colonization and successful reproduction

The arrival of a non-native species does not automatically lead to successful establishment. Unless invaders reproduce clonally, are self compatible, apomictic or parthenogenic, occurring in sufficient numbers is one of the key prerequisites for establishing a founder population (Sax & Brown 2000; Lockwood et al 2005). If the population falls below a minimum population density, called the Allee threshold, it will likely go extinct naturally and the invasion will fail (Liebhold and Tobin, 2008). Many factors may generate Allee effects, such as a decrease in co-operation to find resources and avoid natural enemies, an increase of inbreeding and an increase of reproduction difficulties. In this regard, climatic factors might also have an important role if they can increase the per capita reproductive output for any given population density.

Changes in climatic conditions that result in a prolonged growing and reproductive period often provide conditions that alien species may exploit (Hemerik *et al.* 2004). Species introduced from warmer regions to temperate areas have, until recently, been constrained by too short growing seasons, which prevented several species from becoming naturalized. This could be about to change. There is evidence of a strong association between patterns of the emergence of invasive gypsy moth, *Lymantria dispar,* and climatic suitability in Ontario/Canada (Régnière *et al.*, 2009). The alien moth was trapped more frequently in this region since 1980. However, between 1992 and 1997 a temporary decline in climatic suitability occurred and resulted in a pronounced reduction in the area of defoliation by this species. Since 1998, the trend reversed again with the consequence of resurgence in defoliation and increased frequency of moths in pheromone traps to the north and west in Ontario.

In organisms for which population dynamics are mainly controlled by temperature, climate change may increase development rates and lead to the production of an additional yearly generation (Jönsson *et al.* 2007, Kiritani 2006, Gomi *et al.* 2007). In Japan, recent climate change may have affected the life cycle, life-history traits and, hence, the spread of the American fall webworm, *Hyphantria cunea*. This invasive moth has recently expanded its range, mainly towards the North. In parallel, it shifted from a bivoltine to a trivoltine life-cycle in at least a part of its range, and important changes in some life-history traits, such as the critical photoperiod for diapause induction, have occurred (Gomi *et al.* 2007). In a similar way, the native spruce bark beetle *Ips typographus* is changing voltinism in European mountain forests as a consequence of the disproportionately large warming at high elevations (Lange *et al.*, 2006), with the possibility of producing unprecedented outbreaks, as it happened with the mountain pine beetle *Dendroctonus ponderosae* in British Columbia, Canada (Kurz *et al.*, 2008), and this has potential implications for coniferous plantations elsewhere.

Another key point is the synchrony between the development of host plant and that of the related insect. Studies done on native species showed that climate warming may lead to a mismatch between the two processes because of different thermal thresholds, e.g. for bud burst and egg hatching between oak and winter moth, *Opheroptera brumata* (Visser and Both, 2005), or sycamore aphid (Dixon, 2003). It is likely that the same process is affecting introduced species but it is not yet documented.

From successful reproduction to spread and expansion

Increasingly, native species have exhibited marked natural poleward (and towards higher altitudes as well) movement from warmer regions sometimes at the expense of local resident species that are adapted to colder climates (Williams & Liebhold, 1995; Bale *et al*., 2002). For example, migratory Lepidoptera species in southern Britain are increasing and linked to positive temperature anomalies in spring and summer (Sparks *et al.*, 2007). Similarly, the rapid increase in the establishment of migrant butterflies on Nansei Islands (Japan) in the 20th century is correlated with the elevation of surface temperature (Kiritani, 2006). Furthermore, there is an overall and significant increase of Mediterranean dragonfly species in middle and northern European countries and African species are expanding their range to southern Europe whilst Euro- Siberian species rather show range contractions (Ott 2009). In the same time these species show a change in their voltinism: e.g the damselfly *Ischnura pumilio*, which is in the southern part of its range in Europe trivoltine and in the northern part uni- and semivoltine, now also becomes more and more bivoltine in the latter. Under temperate latitudes, low temperature is usually a key-factor constraining the range expansion through minima thresholds required for the insect survival and development (at different stages: egg, larva and adult). For instance, the lower lethal temperature for the southern pine beetle, *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae), is -16°C, thus winter temperature may limit its northern distribution (Ungerer *et al*., 1999). In the past, presence of the insect in the southern USA effectively matched with the areas where the probability to reach this lethal temperature was low. However, outbreaks occurred recently at the northern limit: for the first time in New-Jersey and Ohio in 2001 and in Maryland in 2005 in relation to the latitudinal shift in winter isotherms (Trần *et al*., 2007).

In addition to these natural expansions of species ranges, global warming may also be responsible for the sudden spread of established alien species, often causing serious economic or ecological hazards. For example, three springtail species accidentally introduced into Marion Island perform better than indigenous springtails in the warmer and dryer climate that this sub-Antarctic island is presently facing (Chown *et al.*, 2007; Slabber *et al.*, 2007). The carabid beetle *Oopterus soledadinus* was accidentally introduced into the Kerguelen Islands (sub-Antarctic) from the Falklands at the beginning of the 20th century. However, it was not before the second half of the century that it started to spread, possibly due to increased temperature and lower precipitation (Chevrier *et al.*, 1997). It has now invaded most regions and has become so abundant that it is threatening the native fauna. The southern green stink bug *Nezara viridula*, formerly a sub-tropical species, has been expanding its range northward in temperate regions of Japan and Europe since the 1960s (Musolin, 2007), probably because of reduced winter mortality resulting from milder winters. In the newly invaded regions in Japan, *N. viridula* has become a major pest, out-competing the indigenous *N. antennata* (Tougou *et al.*, 2009). Thus, climate change may remove/relocate barriers that control spread and so allow for an expansion in areas where the species were previously kept in check by climatic factors (Walther *et al.*, 2002; Battisti *et al.*, 2005). However, the geometry of the expanding bioclimatic envelope may strongly influence this spread. Modelling predicts that invasive species which have a high mobility, although they could more easily follow the migration of the climate envelope, may fail to expand when they face both a local narrowing of the envelope boundary, such as the one generated by Alpine corridors, and an Allee effect (Roques *et al.* 2008). At present, most (78%) exotic insect species already present in Europe are restricted to one or two countries, less than 1% (mostly seed beetles and insects of stored products) having colonized all of the European countries (Roques *et al.*, 2009).

Mechanisms underlying invasion success in the context of climate change

All these aforementioned examples suggest that changing climatic conditions, and warming in particular, appear to have an increasingly important role in triggering increases in population abundance and distribution not only of native but also of alien species in the period with altered climatic conditions since the 1970s. In many cases, an in-depth understanding of the ecological limits of the species and how these have changed during the recent past supports this hypothesis. Such changes are particularly obvious at higher latitudes and altitudes, where previously there were thermal constraints. A remarkable example is the pine processionnary moth, *Thaumetopoea pityocampa* (Lepidoptera: Notodontidae), an originally Mediterranean insect which is currently expanding its range distribution towards higher latitudes and altitudes (Battisti *et al*., 2005). Larval development occurs during winter and is limited by both lethal temperatures (-16°C) and temperatures allowing feeding (i.e. night air temperature below 0°C and temperature inside the nest below 9°C on the preceding day; Battisti *et al.*, 2005). Climatic models based on these thresholds revealed an unfavourable area in the South of the Paris Basin (France), which constrained the insect distribution up to the 1990s. Along with warming up since 2000, the moth is no longer limited by unfavorable larval feeding conditions and succeeded in crossing this area and expanding its range distribution by around 5.6 km per year (Robinet *et al*., 2007).

The same model also showed that warming up may have contradictory effects depending on time (winter vs. summer) and location in relation to the timing of insect development. Whereas the warm winter 2003 triggered larvae survival in newly colonized areas of the Paris Basin, the heat wave of summer 2003 killed a large part of the population in the same area (Robinet *et al.*, in press). Contradictorily, the high temperatures observed in summer 2003 resulted in a significant altitudinal shift of the moth in the Italian Alps (Battisti *et al*., 2006). Indeed, the moths emerged earlier in the first case and egg-masses and first- instar larvae were exposed to extremely high temperatures whilst these temperatures occurred during adult flight in the Alps, and enabled a higher proportion of female moths to disperse at unusually long distances.

These examples show that some alien species profit from ameliorated conditions, mainly owing to warmer temperatures. Much less is known of introductions that failed or species that show range contractions as a consequence of climate change (Parmesan *et al.*, 1999). Moreover, besides temperature, other aspects of climate change, such as changes in precipitation regimes, are also likely to influence invasion processes. There is observational evidence from long-term monitoring data gathered since 1993 suggesting that increase in rainfall promotes a wider distribution of the introduced Argentine ant *Linepithema humile* into new areas in California (Heller *et al.*, 2008). As in the case of climate change impacts on native species, the data on impacts of changing rainfall regimes on alien species is less readily available than of temperature and it remains to be seen whether general, predictable patterns will arise.

The future?

As mentioned above, more than 400 out of the 1315 non-native insect species established in Europe originated from areas with subtropical and/or tropical climate and were thus capable to survive under European winter conditions at least locally, e.g. along the Mediterranean coast. (Roques *et al.*, 2009). Moreover, interceptions at the European borders by quarantine services from 1995 to 2005 revealed that an increasing number of exotic insect species is arriving from the tropics. Thus, 38.7% of intercepted species arrived from tropical Asia (18,2%), tropical and southern Africa (15,2%), south America (5,1%), and Australasia (0,2%) (Roques and Auger- Rozenberg, 2006). The recent arrival and establishment of several tropical species associated with palms is illustrative of this process. Since 1993, 31 palm pests were recorded, among them a Castniidae moth from South America, *Paysandisia archon* (Montagud Alario *et al.* 2004) and the red palm weevil, *Rhynchophorus ferrugineus*, from Melanesia, which successfully colonized southern France, Corsica, Italy, continental Greece, Crete and Cyprus from 2004 to 2006 (Rochat *et al.* 2006). More generally, the colonization of palms, eucalyptus and tropical legume trees planted in Europe significantly increased during the period 2000- 2007 through the establishment of specific, exotic insects whereas that of broad-leaved trees remained stable and that of conifers decreased (Roques, unpublished data). We suggest to keep continuously updated such a survey of the relative importance of the colonized host plants but also of the different insect guilds in order to be capable of noticing as soon as possible the temporal changes and therefore target the pathways and taxa to be especially surveyed.

A number of studies attempted at predicting the suitability of ecosystems for invaders under potential climate warming (e.g., Wharton and Kriticos, 2004; Vanhanen *et al.*, 2008). Using the climatic modeling program CLIMEX, Vanhanen *et al.* (2008) simulated the potential distribution ranges in Europe of three different Asian Cerambycid beetles, *Aeolesthes sarta*, *Tetropium gracilicorne* and *Xylotrechus altaicus*. This program calculates an ecoclimatic index based on the life cycle requirements of a species and thus represents the probability of a viable population existing at a certain location. Simulations showed that the three studied species have a large potential distribution in Europe according to climatic factors. Only one of the three species (*A. sarta*) was predicted to have some difficulties in establishing populations in central and northern parts of Europe but the other two species could become established practically anywhere in Europe except southern parts. Simulation with IPCC climate change scenario A1B resulted in changes of 200 to 1100 km at the northern and southern edges of the distribution range for the studied species. Such modeling approaches may be criticized; e.g., CLIMEX is not good for predicting distribution of species that have an obligatory diapause and whose development takes more than one year; also it is not taking into account local microclimate and local variations in the response of the introduced populations. In contrast, some other modeling studies showed a rather limited influence of global warming, compared to other factors, on expansion of invasive organisms, e.g. the pine wood nematode in China (Robinet *et al.*, 2009).

However, the introduced insect species must in any case find an acceptable host and at the right development stage. Apparently, it is not so easy. About half of the exotic species related to woody plants that were introduced to Europe are still confined to the original, exotic host tree and did not switch to another host plant (Roques *et al.*, 2009). A challenge for further studies is to precise the capabilities of exotic insects to switch on native plants with respect to the response of these plants to global warming in terms of phenological development and change in physical and chemical composition.

Conclusion

Climate change tends to blur invasion and migration processes. The increasing number of colonisation events and subsequent establishment of species originating from regions with a warmer climate than in the area of establishment and spread is remarkable. Such species appear to have responded to the changed climatic conditions of the recent past, which enabled them to reproduce and establish in the presence of resident species. At the same time, native species have also exhibited marked natural poleward movements from warmer regions, sometimes at the expense of local resident species that are adapted to colder climates. However, it is often difficult to disentangle human-mediated movements and natural migration processes. For example, the present northward expansion of the native pine processionary moth probably results from a combination of a natural short-range expansion triggered by climate warming and of long-distance events where moth pupae are carried with the soil accompanying large pine trees translocated by humans as ornamentals (A. Roques, pers. observ.). Other Mediterranean insects, such as the praying mantis, *Mantis religiosa*, and the bush cricket *Meconema meridionale*, are expanding their native range in southern Germany, but they are also found further north, far away from their natural range; these populations are considered to be the result of accidental transport by humans (Ott, 2009). With continued climate change, native species are forced to shift their ranges over ever larger distances and/or depend on human assistance to reach suitable habitats. Hence, in a changing world, it will become increasingly difficult to assess the role of humans in the observed range expansion, especially when species originate from the same continent or adjacent regions, but human assistance in their transfer cannot be excluded. This increases the risk of being perceived in the new habitat as an alien invader. Thus, a crucial distinguishing factor between native and alien species becomes increasingly blurred with continued climate change.

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Literature

Ayres, M.P. and Lombardero, M.J. (2000) Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *The Science of the Total Environment*, 262, 263-286.

Bale, J.S., *et al.* (2002) Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biol.*, 8, 1-16.

Battisti, A., Stastny, M., Netherer, S., Robinet, C., Schopf, A., Roques, A. and Larsson, S. (2005) Expansion of geographic range in the pine processionary moth caused by increased winter temperatures. *Ecol. Appl.*, 15, 2084–2096.

Battisti, A., Stastny, M., Buffo, E. and Larsson, S. (2006) A rapid altitudinal range expansion in the pine processionary moth produced by the 2003 climatic anomaly. *Global Change Biol.*, 12, 662-671.

Chapman, J.W. *et al.* (2008). Wind selection and drift compensation optimize migratory pathways in a high-flying moth. *Curr. Biol*. *18*, 514-518.

Chevrier, M., Vernon, P. and Frenot, Y. (1997). Potential effects of two alien insects on a subantarctic wingless fly in the Kerguelen Islands. In *Antarctic Communities : Species, Structure and Survival* (eds. B. Battaglia, J. Valencia and D. W. H. Walton), pp. 424–431. Cambridge University Press, Cambridge, UK.

Chown SL, *et al.* (2007) Phenotypic plasticity mediates climate change responses among invasive and indigenous arthropods. *Proc. R. Soc. B* 274, 2531-2537.

Coulson S.J., *et al.*. (2002) Aerial colonization of high Arctic islands by invertebrates: the diamondback moth *Plutella xylostell* (Lepidoptera: Yponomeutidae) as a potential indicator species. *Divers. Distrib.* 8, 327-334

Dekoninck W.C. *et al.* (2002). On the arrival of the Asian invader ant *Lasius neglectus* in Belgium (Hymenoptera, Formicidae). *Bull. Soc. Roy. Belg. Entomol.* 138: 45- 48.

Dixon, A.F.G. (2003) Climate change and phenological asynchrony. *Ecol. Entomol.* 28, 380-381.

Eritja, R., *et al.* (2005) Worldwide invasion of vector mosquitoes: present European distribution and challenges for Spain. *Biol. Inv.*, 7, 87-97.

European Environment Agency (2008) *Impacts of Europe's changing climate*. European Environment Agency report. EEA Briefing 3/2008 - Available on line at: http://www.eea.europa.eu/publications/briefing_2008_3

Flemming, R.A. (2000) Climate change and insect disturbance regimes in Canada's boreal forests. *World Resource Review*, 12, 520-543.

Gomi, T. *et al*. (2007) Shifting of the life cycle and life-history traits of the fall webworm in relation to climate change. *Entomol. Exp. Appl.* 125, 179–184

Greenslade, P. *et al*. (1999) Long distance migration of insects to a subantarctic island. *J. Biogeogr.* 26, 1161–1167

Harrington, R. *et al*. (2007) Environmental change and the phenology of European aphids. *Global Change Biol.* 13, 1550–1564

Hart, A.J. *et al*. (2002) Effects of temperature on the establishment potential in the UK of the non-native glasshouse biocontrol agent Macrolophus caliginosus. *Physiol. Entomol.* 27, 112–123

Hatherly, I.S. *et al*. (2005) Use of thermal data as a screen for the establishment potential of non-native biological control agents in the UK. *BioControl* 50, 687–698

Heller, N.E. *et al*. (2008) Rainfall facilitates the spread, and time alters the impact, of the invasive Argentine ant. *Oecologia* 155, 385–395

Hemerik, L. *et al*. (2004) Predicting the temperature-dependent natural population expansion of the western corn rootworm, *Diabrotica virgifera*. *Entomol. Exp. Appl.* 111, 59–69

IPCC (2007) *Climate Change 2007: The Physical Science Basis.* Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (Solomon, S. *et al*., eds), Cambridge University Press

Jönsson, A.M. *et al*. (2007) Impact of climate change on the population dynamics of *Ips typographus* in southern Sweden. *Agric. For. Meteorol.* 146, 70–81

Kenis, M. (2006) Insects-Insecta. In *Invasive Alien Species in Switzerland. An inventory of alien species and their threat to biodiversity and economy in Switzerland* (Wittenberg, R., ed), pp. 131–211, Swiss Confederation - Federal Office for the Environment Environmental Studies 29/6

Kiritani, K. (2006) Predicting impacts of global warming on population dynamics and distribution of arthropods in Japan. *Popul. Ecol*. 48, 5–12

Kobelt, M. and Nentwig, W. (2008) Alien spider introductions to Europe supported by global trade. *Divers. Distrib.* 14, 273–280

Kurz, W.A. *et al*. (2008) Mountain pine beetle and forest carbon feedback to climate change. *Nature* 452, 987–990

Liebhold, A.M., P.C. Tobin. (2008). Population Ecology of Insect Invasions and Their Management. *Ann. Rev. Entomol.* 53:387–408.

Lange, H. *et al*. (2006) Thresholds in the life cycle of the spruce bark beetle under climate change. *Interj. Complex Syst.* 1648

Lockwood, J. L. *et al*. (2005) The role of propagule pressure in explaining species invasions. *Trends Ecol. Evol.* 20, 223–228

Logan, J.A., Regnière, J. and Powell, J.A. (2003) Assessing the impacts of global warming on forest pest dynamics. *Front. Ecol. Env.*, 1, 130–137.

Montagud Alario S; Rodrigo Coll I (2004) *Paysandisia archon* (Burmeister, 1880) (Lepidoptera, Castniidae): nueva plaga de palmáceas en expansión. *Phytoma España*, 157: 40-53.

Musolin, D.L. (2007) Insects in a warmer world: ecological, physiological and life- history responses of true bugs (Heteroptera) to climate change. *Global Change Biol.* 13, 1565–1585

Newman, J.A. (2005). Climate change and the fate of cereal aphids in Southern Britain. *Global Change Biol.*, 11, 940–944

Ott, J. (2009) Effects of climatic changes on dragonflies – results and recent observations in Europe. In *Monitoring climate change with dragonflies*. (Ott, J., ed), in press, Pensoft

Parmesan, C., *et al.* (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, 399, 579-583.

Parmesan, C. and Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37-42.

Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *The Annual Review of Ecol. Evol. Syst.*, 37, 637-669.

Régnière, J. *et al.* (2009) Climate suitability and management of the gypsy moth invasion into Canada. *Biol. Inv.* 11, 135–148

Robinet, C. *et al*. (2007) Modelling the effects of climate change on the potential feeding activity of *Thaumetopoea pityocampa* (Den. & Schiff.) (Lep., Notodontidae) in France. *Global Ecol. Biogeogr.* 16, 460–471

Robinet, C. *et al*. (2009); Role of Human-mediated dispersal in the spread of the pinewwod nematode in China. *PLoS One* 4 (2): e4646. doi:10.1371/ journal.pone.0004646

Rochat D. *et al.* (2006) Le charançon rouge du palmier dans le bassin méditerranéen. *Phytoma- La Défense des Végétaux* 595: 20-24.

Roques, A. *et al*. (2009) Alien terrestrial invertebrates of Europe. In *Handbook of Alien Species in Europe* (Nentwig, W. *et al*. eds), pp. 63–79, Springer

Roques, A. and Auger-Rozenberg, M.-A. (2006) Tentative analysis of the interceptions of nonindigenous organisms in Europe during 1995-2004. *EPPO Bulletin*, 36, 490–496.

Roques, L. *et al*. (2008) Population facing climate change: joint influences of Allee effects and environmental boundary geometry. *Popul. Ecol.* 50, 215–225

Rouault, G., Candau, J.-N., Lieutier, F., Nageleisen, L.-M., Martin, J.-C. and Warzée, N. (2006) Effects of drought and heat on forest insect populations in relation to the 2003 drought in Western Europe. *Ann. For. Sc.* 63, 613–624.

Sala, O.E. *et al.* (2000) Global biodiversity scenarios for the year 2100. *Science* 287, 1770-1774

Sax, D.F. and Brown, J.H. (2000) The paradox of invasion. *Global Ecol. Biogeogr.* 9, 363–371

Simberloff, D. (2000) Global climate change and introduced species in United States forests. *The Science of the Total Environment* 262, 253-261

Slabber S. *et al.* (2007) Acclimation effects on thermal tolerances of springtails from sub-Antarctic Marion Island : Indigenous and invasive species. *J. Insect Physiol*. 53, 113-125

Sparks, T.H. *et al*. (2007) Increased migration of Lepidoptera linked to climate change. *Eur. J. Entomol.* 104, 139–143

Tougou D., Musolin D.L. & Fujisaki K., 2009. Some like it hot! Rapid climate change promotes changes in distribution ranges of *Nezara viridula* and *Nezara antennata* in Japan. *Entomol. Exp. Appl*. 130, 249-258.

Trần, J.K., *et al.* (2007). Impact of minimum winter temperatures on the population dynamics of *Dendroctonus frontalis*. *Ecol. Appl.*, 17, 882–899.

Ungerer, M.J., Ayres, M.P. and Lombardero, M.J. (1999) Climate and the northern distribution limits of *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae). *J. Biogeography*, 26, 1133-1145.

Vanhanen H., Veteli T.O., and Niemelä P. (2008). Potential distribution ranges in Europe for *Aeolesthes sarta*, *Tetropium gracilicorne* and *Xylotrechus altaicus*, a CLIMEX analysis. *EPPO Bulletin* 38: 239-248.

Visser, M. E. and Both, C. (2005) Shifts in phenology due to global climate change: the need for a yardstick. *Proc. Roy. Soc. London, B*, 272, 2561–2569.

Walther, G.-R. *et al.* (2002) Ecological responses to recent climate change. *Nature* 416, 389–395

Ward N.L. and Masters, G.J. (2007). Linking climate change and species invasion: an illustration using insect herbivores. *Global Change Biol.* 13 : 1605-1615

Wharton, T.N. and Kriticos, D.J. (2004) The fundamental and realized niche of the Monterey Pine aphid, *Essigella californica* (Essig) (Hemiptera: Aphididae): implications for managing softwood plantations in Australia. *Divers. Distrib.* 10, 253-262.

Williams, D.W. and Liebhold, A.M. (1995) Forest defoliators and climatic change: potential changes in spatial distribution of outbreaks of western spruce budworm (Lepidoptera: Tortricidae) and gypsy moth (Lepidoptera: Lymantriidae). *Env. Entomol.* 24, 1-9.