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A PERSPECTIVE ON CLIMATE CHANGE AND INVASIVE ALIEN SPECIES

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ABSTRACT

Climate change and other components of global change are already affecting biodiversity, and further changes can be expected. Novel ecosystems are arising in response to human-induced changes (abiotic and biotic) entailing the risk of biotic homogenisation (McKinney & Lockwood 1999; Olden *et al*. 2004). Humans have already "produced" novel ecosystems along the history (Hobbs *et al*. 2006) but current rates of change are much faster. Ecosystems are already changing and presumably a new ecological order will arise in the future. Among the driving elements of global change, the alteration of climate is recognised as one of the most harmful both *per se* and in combination with biotic changes.

Biological invasions are a widespread and significant component of human-caused global environmental change. Biotic invaders interact synergistically with others components of global change, like land use change, increase in nitrogen deposition and in [CO_2], warmer temperatures, increase in the frequency of extreme events such as storms and fire, etc. (see Figure 1) (Dukes & Money 1999).

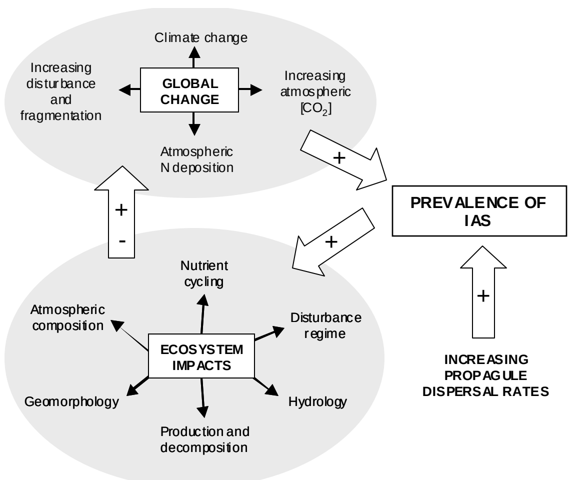

Figure 1. Impacts of global change on biological invasions and feedbacks from invaders to global change.

Modified from Dukes & Money (1999).

Various elements of global change play a role in the success of IAS. Together, these factors lead to increase in the number and abundance of invasive alien species (IAS). Feedbacks on global change will be positive or negative, depending on the invasive species and elements of global change.

There is increasing evidence that climate change will interfere with processes underlying biological invasions, although we should not rush to make specific predictions with the current level of knowledge. Nevertheless, there is a general consensus that climate change will potentially favour invasive alien species (IAS) leading to new invasions and spread of the already established IAS.

Changes in temperatures may stress native species, decreasing the resistance to invasion of natural communities. Likewise, increasing disturbance elements (such as fires, floods, storms, heat-waves, droughts, etc.) as a direct consequence of climate change, could benefit alien species. The rise in [CO_2] will probably alter the prevalence of IAS. Like plants, ecosystems differ in their responses to elevated [CO_2]. If the rise in [CO_2] increases the availability of other resources or causes changes in the fire regime, new IAS could take advantage of the new conditions in the environment. Non-indigenous animals will also be affected by the changes in ecosystems qualities and in their host plants.

Recent research allowed a better understanding of some of the mechanisms that could act as a trigger in promoting invasions. However, the proper biology of the species, the susceptibility to invasion of the host ecosystem, the vulnerability of native species to climate change, and the dynamism of changes in the interactions within ecosystems and human activities, make predictions extremely feeble.

Nevertheless, results given by the different predictive models are outlining a plausible increase in the abundance and impact of new and already established IAS and should be used as guidelines to develop future research and orient policies and decision making.

In conclusion, the importance of individualistic response of species to changing environmental factors, and the importance to produce predictions on a species-by-species basis should be stressed. Future research projects need to include the identification of new potential areas of invasion. In this framework, the present report attempts to address the issue of biological invasions in relation to modern climate change. Without pretending to be a full review of the subject, and based on the review of the more treated organisms in literature (plants, insects and marine species), this report aims at providing a starting point for debate on strategies to be undertaken to face the problem, as well as at generating synergies with other working groups and institutions dealing with the subject.

Key-words: invasive, invasibility, climate change, global change, plants, insects, marine environment, diseases.

INTRODUCTION

Changes in climate are not new phenomena in the history of the Earth which has undergone several successions of glaciations and warming (interglacial periods) driven by natural variability (Houghton *et al*. 1996; Paillard 1998 and 2001). Climate changes, in combination with abiotic and biotic factors (e.g. physical environment, species interactions, etc.), the accessibility of an area to dispersal by species and the adaptability of species to new conditions, affected the geographic distribution of flora and fauna (Soberón & Townsend Peterson 2005).

However, human influences (contaminant emissions, changes in land use, etc.) are altering modern climate leading to a situation that exceeds the limits of natural variability by producing the most rapid global warming event ever recorded in Earth's history (Karl *et al*. 2003; Huntley 2007).

Working Group I of the Intergovernmental Panel on Climate Change (IPCC), stated in its Fourth Assessment Report that "warming of the climate system is unequivocal", and attributing it, on the basis of a higher level of likelihood compared to those adopted in the previous report (> 90% probability against > 66%) to the observed increase in anthropogenic greenhouse gas concentrations since the mid-20th century. Evidence of already visible changes in climate include "the increased global averages of air and ocean temperatures, widespread melting of snow and ice, and rising of global average sea level". Furthermore the report warns that "continued greenhouse gas emissions at or above current rates would cause further warming and induce many changes in the global climate system during the 21st century that would *very likely* (> 90% probability) be larger than those observed during the 20th century" (IPCC 2007).

Taking into account the complexity of the climate system and the interactions among the elements that make it up, it has to be expected a human induced reorganisation of abiotic factors such the ocean-atmosphere system, chemical cycles (e.g. carbon), precipitations, wind patterns, etc., as well as biotic like marine, freshwater and terrestrial ecosystems.

Climate projections from IPCC Working Group I indicate that annual mean temperatures in Europe are likely to increase more than the global mean (a variation from 2.3°C to 5.3°C in Northern Europe and from 2.2°C to 5.1°C in Southern Europe under the basic A1B scenario) (Christensen *et al*. 2007).

Northern Europe will register higher minimum winter temperature (more than the average), having its largest warming period in this season, while Central and Southern Europe will present the largest warming in summer with an increase above average in maximum summer temperatures (likelihood level > 66%) (Christensen *et al*. 2007).

Results of the report related to precipitation point to marked differences between different parts of the European continent. The annual number of precipitation days and extremes of daily precipitation are expected to increase in the North and Centre of Europe (only in winter in the latter area) (likelihood level > 99% and >66% respectively) whereas a decrease is expected in Southern Europe as well as in Central Europe (only in summer in the latter area) (likelihood level > 99% and >66% respectively) with a higher risk of summer droughts (likelihood level > 99%) (Christensen *et al*. 2007).

The snow season will be shorter (likelihood level > 99%) accompanied by a decrease in snow depth (likelihood level > 66%) in most of Europe (Christensen *et al*. 2007).

Data on changes in future windiness are not supported by a high level of confidence. However the pointed trend is an increase in wind strength in Northern Europe (Christensen *et al*. 2007).

The influence of climate changes on biodiversity is not questionable. Species' responses to past changes in climate are proven by the fossil record that highlights the spatial response (changes in distribution patterns) as one of the most important consequence. Genetic variance and adaptability were key factors in determining the magnitude of species displacement and their survival or extinction (Huntley 2007).

Moreover, Huntley (2007) proposes a hierarchical approach based on spatial and temporal scales in order to understand the extent of species' responses to climate change which are categorised as follows: behavioural responses, population dynamic responses, adaptive genetic responses, spatial responses and macro-evolutionary responses.

However, the individualistic nature of species' responses has to be taken into account when it comes to analyse or predict the effects of modern climate change on species distribution because it could ultimately affect the whole ecosystem through quantitative and qualitative changes in communities' structure and composition, with the added risks of a cascade effects (Huntley 2007).

Effects of modern climate change on biodiversity are already occurring (Usher 2005; Alcamo *et al*. 2007), such as human induced temperature patterns associated with changes in animal and plants phenology and distribution (Walther *et al*. 2002; Root *et al*. 2005).

In a study on non-migratory British butterflies, Warren *et al*. (2001) found that mobile and generalist species increased their distribution in the last three decades consistently with a climate explanation. Parmesan and Yohe (2003) found a clear climate fingerprint in a temporal and spatial switch of 279 species. Observations carried out through a systematic phenological network data set (more than 100000 observational series of 542 plants species) in 21 European countries for the period 1971-2000 provided evidences of earlier leaf unfolding, flowering and fruiting in wild European plants (Menzel *et al*. 2006). In Britain, Hickling *et al*. (2006) reported the shift in the distribution of 327/329 species belonging to 16 different taxa of fauna. Compelling evidence of climate changes impacts on migratory species (temporal and spatial shifts, changes in prey distribution, the timing of parts of the life cycle, breeding success, etc.) is provided by Robinson *et al*. 2005.

Two Europe-wide assessments of European flora and fauna (amphibians and reptiles) under various scenarios indicated the importance of dispersion to avoid a reduction in their distribution range and the risk of becoming seriously threatened with extinction (Thuiller *et al*. 2005; Araújo *et al*. 2006).

Inland freshwater system species' richness will be dominated by drought regimes leading, under the projected scenarios, to an increase in the North of Europe and a decrease in the South-West of the continent (Alcamo *et al*. 2007).

Recent research on the effects of climate change in marine ecosystems report the decline of sea-ice cover in northern seas, a spatial shift of southern species' populations northwards replacing northern species, and exceptionally high temperatures in European marine waters (with the exception of the Black Sea) (Philippart *et al*. 2007). Changes in temperature or in the frequency of inflow have been particularly noxious for enclosed seas ecosystems (e.g. alteration of plankton composition and food web in western Mediterranean, increase of thermophilic species of ichthyofauna in the Adriatic Sea, etc.), which have suffered a greater impact than the open seas (Dulcic & Grbec 2000; Molinero *et al*. 2005; Philippart *et al*. 2007).

Current efforts in research are devoted to understand and predict how climate change will affect biodiversity under different scenarios in order to develop strategies oriented to the management of wildlife and habitats. However, this is not an easy task because of the difficulty to predict species' responses (which are individualistic) (Huntley 2007) and the complexity of interactions between the effects of climate change with other elements of global change (changes in land use, atmospheric composition, nitrogen deposition, etc.), which are affecting native species' distribution and ecosystem dynamics as well as non-native species (Dukes & Mooney 1999).

Bioclimatic models have been largely used to predict the impact of climate change on biodiversity providing useful approximations on the future distribution of species. However, their validity has been questioned by several authors who stressed the importance of factors other than climate (e.g. biotic interactions, evolutionary change and dispersal ability) as influencing species distributions, as well as the importance of the spatial scale at which these models are applied (Davis *et al*. 1998 a,b; Lawton 2000; Pearson & Dawson 2003).

Biotic interactions such as competition, predation and symbiosis could affect the distribution of species (directly and indirectly). However, their effect can be minimised by applying bioclimatic models at a large scale because of the dominant role of climate (Pearson & Dawson 2003).

Ecosystems' shift in response to global climate change could be followed by a dramatic variation in the nature and timing of life-cycle processes and trophic interactions. In this framework, the role of primary producers in shifting ecosystems (bottom-up perspective) as a consequence of global warming has been investigated at length, while animal species "have been pushed into the background" expecting them to redistribute themselves by following plants shift. However, shifts in ecosystems driven by top predators (top-down effect) have been detected highlighting the role of higher-order trophic interactions in moulding ecosystem structure and functions as a consequence of global warming (Schmitz *et al*. 2003).

Changes in species distribution and behaviour due to changes in climate have already been observed and are generally attributed to phenotypic plasticity (Bradshaw & Holzapfel 2006). Genetic changes have been scarcely taken into account because they are expected to occur only on long time scales. Bioclimate models assume that extinction rates are faster than adaptation rates (Pearson & Dawson 2003). However, recent studies pointed out that genetic changes induced by climate change in species populations.

Bradshaw & Holzapfel (2001) provided evidence for a genetic response by documenting changes in the photoperiodic response of the pitcher-plant mosquito (*Wyeomyia smithii*). Likewise, Réale *et al*. (2003) have found that the timing of breeding in a Canadian population of North American red squirrel (*Tamiascurus hudsonicus*) has advanced as a result of both phenotypic and genetic changes in response to a rapidly changing environment. A long-term study of a Dutch population of Great tits (*Parus major*) has revealed heritable variation in individual plasticity and in the timing of reproduction (high plastic individuals were favoured by selection) in response to a mismatch between the breeding time of the birds and their prey, concurrent with changes in climate (Nussey *et al*. 2005). This fact adds uncertainty when it comes to predict the effects of climate change for short-lived species and good dispersers which are more able to undergo rapid evolutionary change.

Furthermore, limitations to the bioclimatic modelling approach (erroneous predictions of future species distributions) also arise when species dispersal is taken into account because the movement of species, which depends on its proper biological characteristics, could be also limited by the presence of natural and dynamic artificial barriers where dispersal is occurring (Pearson & Dawson 2003).

Under this perspective, bioclimatic models are recognised as being very useful to make large scale predictions on the potential magnitude and broad pattern of future impacts of climate change, but smaller scale predictions will require the integration of interactions between the complexity of factors affecting species distributions (e.g. climate, land use change, species dispersal, etc.) (Pearson & Dawson 2003).

If predicting accurately the effect of climate change on native species is difficult, it could become even a more complex task for non-native species. The current distribution of non-native species may not be in equilibrium with the current climate, nor indeed their potential establishment and/or spread could be necessarily determined primarily by climate. The way alien species turn into invasive could depend on many factors other than climate (ecosystem resilience, biotic interactions, etc.), as well as the fact that their dispersal counts not only on natural mechanisms (self-dispersal) but also on a large amount of man-made pathways and vectors. It has to be supposed that a huge movement of species (among them pest, infectious diseases, etc.) will accompany human beings displaced by the impact of global warming (up to 150 million people by 2050) (Dupont & Pearman 2006; Low 2008).

Present and latent invasive species' behaviour is difficult to predict under climate change because changing conditions could act as a negative or positive trigger by themselves or in combination with other factors representing or not a limit to species ranges, and therefore their future distributions could show very different realised niches.

Little attention is still given to the risk of evolutionary changes posed by alien species once they become established in a new territory, where they are subject to selective pressures and hybridisation, and which could lead to a rapid evolutionary change. The risk is also increased by the introduction of organisms selected through genetic engineering techniques (e.g. tolerant to pesticides, diseases resistant, etc.) with relatives that are wild species that could turn into weed. Furthermore, alien populations could accelerate evolutionary changes by native species (Cox 2004). In this context, predicting their genetic adaptation in response to new dynamic environments presents a further serious challenge to modellers.

The supposition that the problem of biological invasion will get worse due to climate change, appears strongly supported (Mooney & Hobbs 2000). There is a whole series of processes that are changing, all of which most likely will accelerate the mixing of the world's biota and increase the number of IAS (Mooney & Hobbs, 2000). With climate change, non-indigenous species may cross frontiers and become new elements of the biota (Walther *et al*. 2002). While human activities promote species movement, their subsequent survival, reproduction and spread at the new location imply altered site conditions due, for example, to climate change. (Walther *et al*. 2002). The nitrogen deposition, increased CO_2 concentration in the atmosphere, global warming, fire frequency, changes in precipitation patterns, together with land use modification will play an increasing role in the success of invasive alien species (Mooney & Hobbs 2000). Examples include warm-water species that have recently appeared in the Mediterranean, thermopiles plants that spread from "captivity" into nature, or the immigration of unwanted neighbours such as vector-borne diseases (Walther *et al*. 2002).

Climate change has the potential to modify the impact of IAS by affecting their sources, pathways and destinations (see Fig. 2) (Hobbs & Mooney 2005). If climate change alters any factor of the invasion process (including its interactions), IAS could benefit from these new conditions. In this context, it is important to detect which points of the invasion process could be affected by climate change.

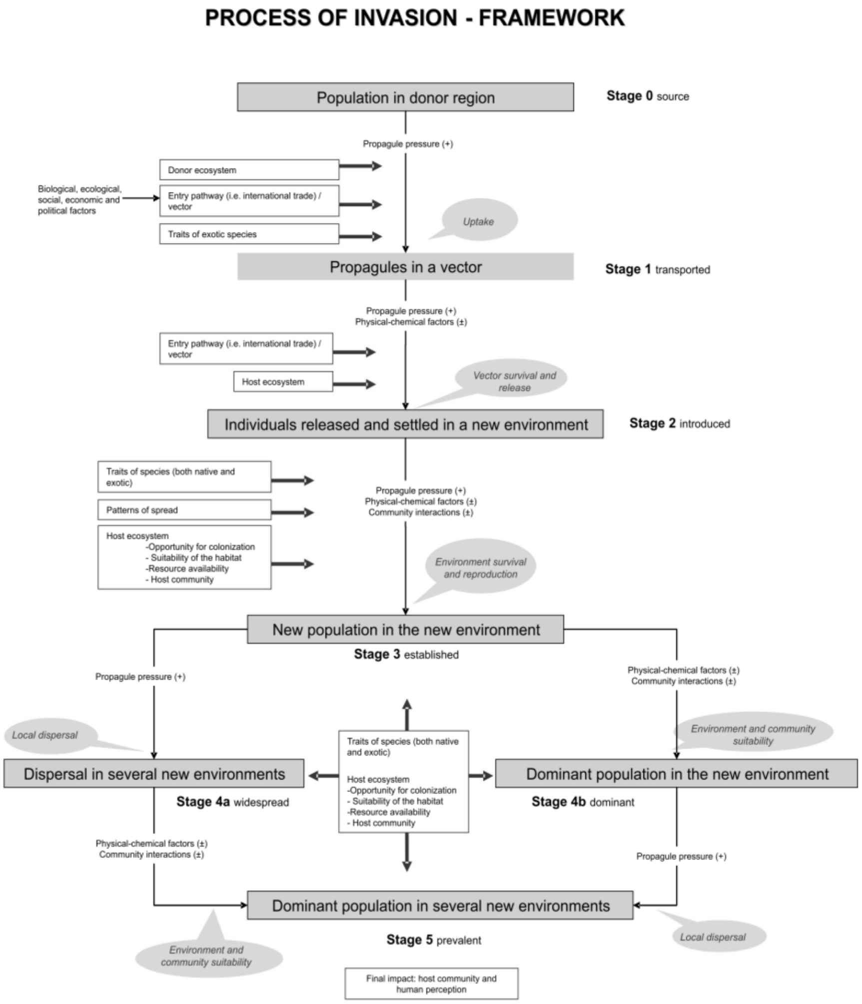

Figure 2. Process of invasion. Framework. (Modified from Occhipinti-Ambrogi 2007).

Climate change influences invasive species by affecting their entry pathways, establishment, spread and colonisation of new habitats. It is important to underline that there is potential for some species that are currently non-invasive to become invasive in native ecosystems due to climate change but others, currently invasive, could turn into greater or reduced threats.

Climate change *per se* is likely to have limited direct effects on movement of IAS along trade routes. But, for example, new patterns of international trade in response to changes in climatic conditions have the potential to alter the composition of invasive species that are disseminating around the world.

Patterns of spread are determined by the species involved, the suitability of the host ecosystem for propagation, and the incidence of extreme climatic events. Storms, prolonged rainy seasons and flooding, etc. determine the dispersal of many invaders. Wind systems affect long-distance migration routes; wind shifts caused by changes in climate have the potential to affect the patterns of migration of some pests such as locusts or moths, etc. Moreover, climatic gradients are likely to play a role in determining the rate and direction of spread of IAS. Disturbances and land transformations offer new opportunities for new species to colonise and spread. Indeed, land-use changes are often brought about by the use of introduced species (new forage species, plantation trees, etc.).

Numerous IAS are dependent on the disturbance of native ecosystems to support their colonisation and establishment. Invasion success is also determined by certain traits of the host ecosystem: opportunity for colonisation, changes in atmospheric patterns, suitability of the habitat, resource availability and the host community, all play an important role. The ecological resistance of an ecosystem to invasion could decrease because of climate change. Extreme events (for example, severe and prolonged droughts) linked to climate change may cause important impact on biological systems because they reduce the resistance to invasion of indigenous species.

Regarding ecosystem perturbations, Low (2008) highlights that some native species could be favoured by new climatic conditions at the expense of other native species. For example warmer conditions have favoured the attack of pine processionary caterpillar on relict stands of Scots Pine in southern Spain (Hódar *et al*. 2002). In the Rocky Mountain area (United States), the increase in the abundance of the mountain pine beetle, which has doubled its capacity of reproduction in response to warmer temperature, is favouring the transmission of a fungus to American conifers (Parmesan 2006; Low 2008).

This fact imposes a series of management problems like having to take into account the risk of translocation of the more disadvantaged species, as well as the ecological conditions created by the new dominant species that could act as a trigger for potential and invasive non-native species (Low 2008).

Changes in land-use patterns that increase habitat fragmentation and alter disturbance regimes will increase the prevalence of non-native species (Dukes & Mooney 1999; (Hobbs & Mooney 2005). In a fragmented and degraded landscape experiencing rapid environmental change, the niches available to IAS could increase. Land transformation acts to encourage biotic change by causing system changes that provide the opportunity for biological invasion, and by bringing new species from different biogeographical regions into contact with these altered systems.

The inherent traits of species (both native and exotic) can play a role in the impact of non-indigenous species. Species characteristics include the number of seed/propagules produced per generation, diet breadth, size of home range, ability to fix nitrogen, overall body size, adaptation to fire, degree of polyploidy, etc. But species traits are not a determining factor in order to predict whether one species has the potential to be a good invader or not. Nevertheless, it is possible to detect some traits that could play an important role in 'predicting' future invasive success.

Invasion processes are a complicated sequence of events and there are many uncertainties… Each stage of the invasion process is characterised by unique ecological and social factors. Invasion processes linked to climate change can bring out some questions that need to be resolved in the future (Dukes & Mooney 1999):

How entry pathways of invaders could be affected by climate change?

Will some ecosystems become more or less susceptible to be invaded?

Will some non-indigenous species that are currently benign become invasive?

Will impacts of existing invaders decrease or become more severe?

Further consideration to be taken into account is that the effect of climate change on the risks from IAS will depend on the sensitivity of the species to climate and the specific host ecosystem and region, making difficult to point out without a doubt which species could be more or less harmful. Given this level of uncertainty, prevention of invasions (and the process of risk minimisation) is of vital importance. The identification of high-risk potential invasive species, their early detection and rapid response, will enhance effective management. Biosecurity strategies will also need to increasingly incorporate climate change projections into risk management assessments.

How climate change influences biological invasions leaves considerable room for interdisciplinary groups to contribute to research. Research is crucial to understand interactions between climate change and biological invasions. However, IAS and their consequences are a present problem which requires not only a theoretical but also an operative and pragmatic approach.

TERRESTRIAL ECOSYSTEMS

PLANTS

There is a general consensus that climate change will potentially favour invasive alien species (IAS) leading to new invasions and spread of the already established IAS (Thuiller *et al*. 2007).

Changes in temperatures may stress native species, decreasing the resistance to invasion of natural communities. Likewise, increasing disturbance elements such as fires which are a direct consequence of climate change (e.g. because of reduced precipitations), could benefit alien species (Myers *et al*. 2004; Grigulis *et al*. 2005).

To predict the impact of climate change on alien plants is far from easy, because of the proper biology of the species that determines responses to different stimulus (e.g. nitrogen and carbon dioxide concentrations, temperature, humidity, etc.), the susceptibility to invasion of the host ecosystem, and the vulnerability of native species to climate change (Dukes & Mooney 1999; Myers *et al*. 2004; Thuiller *et al.* 2007).

Although research has advanced in the understanding of attributes of successful plant invaders, invasibility of plant communities, interactions between habitat compatibility and propagule pressure, residence time, etc., the enormous complexity of these determinants (Rejmánek *et al.* 2005) and existing uncertainties still influence our capacity to predict whether or not an IAS could turn into invasive and its impacts. Therefore it is intuitive that new variables introduced by climate change hinder our progress in achieving precise predictions for IAS.

Climate change could affect the dynamic of plant invasions in two different ways: **a)** by causing alterations in native ecosystems leading to the establishment and spread of invasive alien plants, and **b)** by favouring individual traits of particular IAS.

Climate change could affect native communities by limiting or benefiting particular species and altering inter-specific relations at all levels. **The loss of keystone species or functional groups of plants could profoundly influence the degree of vulnerability to invasion of native communities** (Zavaleta & Hulvey 2004). Moreover, such changes could be very prejudicial because of the generation of feedback effects on ecosystems.

The effects of climate change have been projected for the distribution of 1,350 European plant species for the late 21st century. The results show that the worst scenario would lead to a mean species loss of 42% and a turnover of 63% (Thuiller *et al*. 2005), making predictable profound alterations in communities and ecosystems.

Alterations in native communities may be produced by climate change in many ways: Changes in temperature, precipitation, moisture, level of CO_2 and nitrogen deposition, could act as factors of selection (positive or negative) on plants unbalancing ecosystems by changing dominance equilibrium as well as by interactions between species (at all levels), and with the environment.

As climate change implies altered conditions by changing the disturbance regime of native ecosystems (Pickett & White 1985), it is highly probable that it could provide suitable conditions for the establishment and spread of alien species either new or already established but quiescent (Walther *et al.* 2002; Thuiller *et al*. 2007).

Thus, concerning biological invasions, it becomes clear that **climate change *per se as* well as in combination with other global changes** (land use changes and biotic changes) **has a potential trigger effect on invasion processes** (Mooney & Hobbs 2000; Thuiller *et al*. 2007).

The adaptability of invasive alien species to new environmental conditions is a key factor in the success or failure of an invasion. In this context, climate change involves several aspects having a selective strength on plant traits, such as, the increase in temperatures, changes in rainfall and evapotransportation patterns, and increasing CO_2 (Barrett 2000).

Flora species' response to increased temperatures seems to be mainly phenological compared to that of animal species where range shifts have been clearly detected (Parmesan & Yohe 2003; Hickling *et al*. 2006; Parmesan 2006; Tuiller *et al*. 2007). However, some exceptions are reported in literature. Colonisation from the South of 77 new epiphytic lichens, and the increase in abundance of combined terrestrial and epiphytic lichen species between 1979 and 2001, is reported by Van Herk *et al*. (2002). The spread of shrub species into the tundra is reported by Sturm *et al*. (2005). Numerous case studies from European countries on recent climatic shifts in vegetation have been reported by

Klötzli & Walther (1999). Upward tree-limit shifts have been recorded in Sweden (Kullman 2000 and 2001) and Russia (Meshinev *et al*. 2000; Moiseev & Shiyatov 2003). However, Thuiller *et al*. (2007) point to a major slowness in range shifts of plants than animals.

Evidences of phenological changes have been provided by Menzel et al. (2006) Through an analysis of 254 mean national time series carried out in 21 European countries, the authors concluded that temperatures of the preceding months influence the phenology of species (mean advance of spring/summer by 2.5 days $ºC^{-1}$, delay of leaf colouring and fall by 1.0 day C^{-1}). A significant correlation was found among observed changes in spring and measured national warming across 19 countries.

A **longer growing season** could influence species' reproductive capacity (increased seed production and biomass) and higher temperatures could improve plants' fertility, resulting in increased population sizes. Animal pollinated invasive plants could benefit from this situation showing an increase in fruit and seed set because of the major insect activity due to higher temperatures and longer summer period (Barrett 2000).

However, increasing asynchrony in predator-prey and insect-plant systems due to changes in phenological response between interacting species could have detrimental impacts (Parmesan 2006).

Temperature (minimum temperature) and length of the growing season have been found to control the distribution of two invasive plants in Northwestern Europe: both variables apply in the case of *Fallopia japonica* (Japanese knotweed), while only the length of the growing season is relevant for *Impatiens glandulifera* (Himalayan balsam) (Beerling 1993). However, the author suggests that ecological interactions could have an important role that has to be taken into account in this kind of analysis.

Likewise, Walther *et al*. (2007) suggest that the rejuvenation of the palm *Trachycarpus. fortunei* in Europe, but more expanded in other countries (Australia, Japan, New Zealand and United States), should be considered as an "early stage of a potential invasion" driven by changes in winter temperature and growing season length, indicating also that palms in general are a good global indicator of the warmer conditions.

Aquatic invasive alien plants could benefit from the increasing seasonality and more marked wet and dry cycles. Fewer winter frost and fluctuations in water levels may cause the expansion of IAS such as the Water hyacinth (*Eichhornia crassipes*) leading to an invasion that could be exacerbated by the introduction of frost resistant plants currently being produced in Holland for the horticultural trade (PlantLife 2005). Moreover, an ameliorating climate could cause a burst of Water hyacinth sexual activity, usually reproducing by clonal propagation in invaded areas – a common trait in aquatic weeds – leading to increased amount of genetic variability that could augment its resistance (Barrett 2000).

Warmer and drier summer are likely to increase **algal blooms** of the water-net (*Hydrodictyon reticulatum*) – a species that has spread during the last 15 years due to changes in seasonality and low river flows – and 'blanket weed' (*Cladophora glomerata*) in water bodies of the United Kingdom (PlantLife 2005).

Different conceptual models with diverse level of complexity are used to predict species distribution under climate change scenarios. In spite of their limitation in representing and including the enormous complexity of ecosystems' interacting elements (abiotic and biotic), they provide useful guidelines to understand the consequences of climate change on ecosystems.

By means of simulated projections of vegetation dynamics including invasive plants (tree type and herb type) to test how climate change could promote biological invasion in Mediterranean islands Gritti *et al*. (2006) found that the effect of climate change alone is likely to be unimportant in most of the analysed ecosystems, but stressed the importance of its interaction with CO_2. Invasions were found highly dependent on the initial ecosystem composition and local environmental conditions, being the rate of ecosystem disturbance the main factor controlling the susceptibility to invasion in the short term.

In general, models reveal that: **1)** different elements could act in combination (Zavaleta & Royval 2002; Gritti *et al*. 2006); **2)** effects of climate change are likely to produce severe alterations on native communities that could lead to further changes in their composition, structure and functions, opening the way to opportunistic species (Thuiller *et al*. 2007); **3)** simulated climate change negative impacts on native ecosystems are likely to facilitate invasions (Thuiller *et al*. 2007).

However, **the importance of the individualistic response of species** to changing environmental factors, and therefore the importance to produce predictions on a species by species basis, should be stressed.

Effects of increased concentrations of carbon dioxide are difficult to predict without taking into account the species and the community where they live (Dukes 2000). Invasive plants grown individually respond positively to high level of CO_2 (more efficiently those that use the C_3 photosynthetic pathway compared to those that use C_4 and CAM pathways), but their response change in the presence of other species (Dukes 1999 and 2000). Among plants using C_3 pathway, species in symbiosis with **nitrogen-fixing microbes** respond strongly to elevated [CO_2], in both conditions. However, responses of native and invasive species of the same type are not statistically different in competition-free environments (Dukes 2000).

Experiments in grassland communities carried out by Potvin and Vasseur (1997) and Vasseur and Potvin (1998) indicate that the early-successional species (as many invasive plants are) persistence in a community is favoured by the rise in [CO_2] which slow down the process of succession.

Separately **C_3 plants respond more positively than C_4** but **species' responses change in mixed C_3-C_4** communities depending on other factors, e.g. water, nutrients and light availability, temperature, the efficiency of species in using resources, etc. making difficult the prediction of which species will be the most favoured (Dukes 2000).

The way plants respond to elevated [CO_2] could produce changes in ecosystems giving advantages to some species over others and increasing the chance of invasions.

Plant water-use efficiency rises under high concentration of CO_2 because of the reduction in stomatal conductance, increasing as a consequence of soil moisture. This could be an advantage for species limited by water availability (Dukes 2000). Plants' responses to reduced evapotranspiration could be either **a)** a decrease in the depletion rate of soil moisture that could extend the growth period in dry climates, or **b)** similar depletion rate of soil moisture but increase in biomass production per unit of water transpired. (Kriticos *et al*. 2003).

Elevated [CO_2] can induce plant-mediated alterations in decomposition processes and shifts in soil microbial community (Dukes 2000; Kao-Kniffin & Balser 2007). Alterations in litter decomposition can influence the **accessibility of nutrients** to plants and microbes (Dukes 2000). Furthermore, as atmospheric [CO_2] influences root exudation quantitatively and qualitatively (Paterson *et al.* 1996; Pendall *et al.* 2004), changes in these patterns are like to influence the activity and the composition of **microbial communities** (Kao-Kniffin & Balser 2007).

Alterations in nutrient availability may depend largely on the species that compose a community due to difference in plants' responses to [CO_2] (Hungate *et al*. 1996), in addition to N and invasions levels variations for belowground properties (Kao-Kniffin & Balser 2007).

Thus, it is clear that change in dominant species within a community due to variations in [CO_2] levels (e.g. fast-growing C3 plants combined with the large belowground biomass of many invasive clonal dominants) could affect the availability of nutrients (Dukes 2000) and change belowground properties having an impact on ecosystem functioning (Kao-Kniffin & Balser 2007).

Climate warming and forecasted drier conditions are believed to prolong droughts and increase fire risk (Alcamo *et al*. 2007).

Interactions among changing forest vegetation, climate and fires have been explored under projected climate change conditions for the 21st century in Switzerland. Results indicate vegetation shifts, changes in biomass distribution, increase of summer drought and highest probability of fire occurrence suggesting the importance of including fire disturbance in investigation on landscape dynamics (Schumacher & Bugmann 2006).

Thus, taking into account the combination of rising temperatures and CO_2, that stimulates plant growth and litter accumulation, an increase in fire frequency is very likely (Dukes 2000).

Changing fire regimes together with the loss of native plants generate opportunities for new species (among them IAS) to colonise and become dominant in a new area, establishing a positive feedback between invaders and the fire cycle where invasive plants change fire regimes and then prosper under the new conditions (D'Antonio 2000; Brooks *et al*. 2004).

A multiphase model describing mechanisms underlying interactions between fire cycle and plant invaders has been fully described by Brooks *et al*. (2004) making patently obvious the risk that they entail for the conservation of native biodiversity and the need of management actions.

The threat of this feed-forward process among invasive plants and the fire cycle has been shown by Grigulis *et al*. (2005) in the Northern Mediterranean Basin (a high fire risk area, see Alcamo *et al*. 2007) for the tussock grass *Ampelodesmos mauritanica*.

Further changes in the composition and structure of ecosystems could be promoted by **extreme events** such floods, storms, heat-waves, droughts, etc. acting as disturbance elements, therefore increasing the risk of new invasions (Alcamo *et al*. 2007; Thuiller *et al*. 2007). In this framework, urban areas, where many invasive alien plants are already benefiting from the more favourable climate (Sukopp & Wurzel 2003), could act as reservoirs of invaders as well as protected environments like greenhouses (Thuiller *et al*. 2007).

Of particular concern is the use of **biofuel crops** as an alternative to fossil fuels. Their value has been hardly criticised for many reasons (Low & Booth 2007):

- their cultivation on a large scale will cause the further fragmentation and destruction of natural habitats (e.g. destruction of rainforest to grow biofuel crops), the depletion and eutrophication of scarce water resources, and the increase in the use of fertilisers and pesticides.
- Reductions in greenhouse gas emissions are minimal or non-existent due to the high requirement of energy they have (e.g. the corn as biofuel in the United States).
- Competition with food crops for arable land (e.g. a 10% substitution of petrol and diesel fuel would require 38% of current cropland area in Europe (International Energy Authority (2004)).
- Their potential to turn into invasive.

Regarding the role of biofuel crops as potential invaders, Raghu *et al*. (2006) highlighted that their ideal traits are common to invasive alien species (e.g. high water use efficiency, rapid growth to outcompete other plants, etc.). These authors also emphasise how well known invasive alien species have been considered for biofuel production, such as *Arundo donax* which is listed as one of the 100 world's worst invasive alien species by the ISSG/IUCN, as well as *Miscanthus* × *giganteus* and *Panicum virgatum* which are species with great invasive potential.

In order to face the growing demand for biofuel plants and guarantee that the proposed species for introductions are safe, it is mandatory that costs and benefits analysis also include also environmental risks and costs.

INSECTS

The size of the range occupied by a species at any one time is determined by several ecological factors, including habitat availability, climatic and other environmental parameters (Cannon 1998). Insects are strongly influenced by climate, especially temperature: life cycle duration, voltinism, population density, size, genetic composition, etc., can vary in response to the change of temperature (Bale *et al*. 2002; Ward & Masters 2007). The distribution of many species is limited by summer heat availability rather than the lethal effect of extreme temperatures (Bale *et al.* 2002). Therefore, predicted climatic changes are expected to take part in the range of expansion/contraction of insects, affecting their phenology and altering their rates of growth and development (Bale *et al*. 2002; Ward & Masters 2007).

The **responses of insects** to climate change are expected to be complex and diverse, depending on the **life-history** of the insect and **host plant growth strategy** (Bale *et al.* 2002). It is possible to propose some **traits** that may be important in predicting future invasive success: generalist feeders, cosmopolitan species, multivoltine species, phenotypical plasticity, etc. Species that hold a number of these traits could be favoured by climate change, and may represent a risk in the future (Ward &

Masters 2007). Nevertheless, the traits of insect species are only one determinant of invasion success: opportunity for colonisation, propagule pressure, suitability of the habitat (and, consequently, biotic resistance), and the host community also play an important role (Simberloff 1989; Williamson 1996; Lockwood *et al*. 2005). This is the reason why research on invasive species responses to climate change is a challenge for scientists, as climate affects the invasion process in a diverse way, indirectly as well as directly (Fig. 1) (Ward & Masters 2007).

On the one hand, climate change can have a positive or negative effect on each factor and, on the other hand, different combinations of positive and negative impacts can produce very different levels of invasion success. In order to assess the impact of climate change on insect invasions, Ward & Masters (2007) point out the need to examine each of these factors (see Fig. 3):

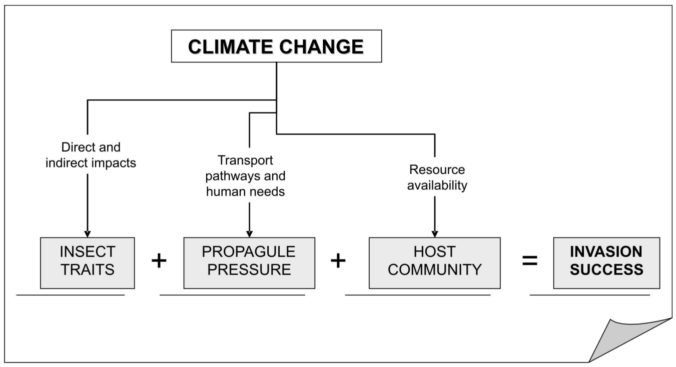

Figure 3. Mechanisms through which climate affects the invasion process of insects (Modified from Ward & Masters 2007).

A. Insect traits.

A1. Diet breadth

Diet breadth has often been linked to the invasion success of insects. **Generalist feeders** (herbivores insects that feed on a variety of plant species) have a higher probability of finding a suitable host plant than those that are specialist and restricted to one or a small number of host plants (Ward & Masters 2007). Presumably, **specialist feeders** will have to move polewards with a changing climate and stay on the single host species in order to survive (Andrew & Hughes 2004).

Similarly, with climate change it is also expected that **cosmopolitan species** (species that have a broader host range and species found at more than one latitude) may be quite resilient to changes in local climate and changes in the distribution of hosts, and are more likely to continue to find suitable host plants (Andrew & Hughes 2004). Likewise, Bale *et al.* (2002) point out that species which currently have wide latitudinal ranges, already encounter considerable temperature variation and are, in a sense, pre-adapted to cope with temperature change. These species will survive *in situ* and/or could move with the host plant and potentially expand their range (Andrew & Hughes 2004). This may be especially true if their current host plant range includes host plants with poor quality (Ward & Masters 2007).

In spite of this, we need to consider that rising concentrations of CO_2 increase C:N ratios of plants (Harrington *et al*. 2001) reducing inevitably the nutritive value of host plants (Cannon 1998). Although generalist insects may have a wider choice of host plants to feed on, they may be less able than specialists to deal with a general reduction in nitrogen and increased concentrations of phenolic compounds, as predicted under CO_2 enrichment (Ward & Masters 2007). In this case, insects need to eat more in order to get adequate dietary nitrogen (Harrington *et al.* 2001). Nevertheless, it appears that in many cases increased feeding rates do not compensate fully for the reduced quality of the diet (Harrington *et al*. 2001). This could be a disadvantage for some insect guilds (for example, sap shuckers) that might not respond by compensatory feeding (Ward & Masters 2007).

A2. Phenological plasticity

The majority of herbivorous insects rely on close synchrony with their host plant to successfully complete their life cycle. Habitually there are key periods during which the host plant becomes appropriate (Ward & Masters 2007). Evidence for an earlier onset of spring phenological events (budburst and flowering), is accumulating in many species and has been related to climate change (Fitter & Fitter 2002). These shifts in the timing of these events are expected to become more marked with climate change. Because of it, phenological uncoupling will take place when climate change will have different impacts on insects and their host plants. This will be unfavourable to herbivore species, such as the gypsy moth, that are tied to specific phenological windows (Ward & Masters 2007). So, **phenological synchrony** of an invader with its host plant in a new place can be of benefit to the invader (Ward & Masters 2007).

With climate change, springs arrive earlier and the growing season is expected to become extended. This fact will be positive to **multivoltine species** because they may be able to produce a larger number of generations in an annual cycle (Ward & Masters 2007). A longer growing season makes also possible a greater number of species to feed on a single host.

Summarizing, phenotypical plasticity of non indigenous species that are not dependent on close phenological coupling with host plants (including multivoltine species), or those responding to similar cues as their host plant, should make better invaders (Ward & Masters 2007).

A3. Lifecycle strategy

For insect herbivores, the ability to complete their life cycle represents a successful adaptation to their host plant and the climatic environment in which they are found (Bale *et al.* 2002). Climate can act directly on insects either as a mortality factor or by determining the rate of growth and development.

Many researchers have predicted that increasing temperatures will lead to increasing winter survival and increasing numbers of generations per year, thus greatly increasing pest pressures (Simberloff 2000). Within a favoured temperature range, temperature elevation increases the speed of development during the growth phase but the rate of increase differs between species (Bale *et al.* 2002). In areas where temperatures affecting physiological processes tend to be below species optima for most of the year, increases in temperature may be expected to speed up these processes and lead to more rapid development, more generations in a season, more movement, and reduced mortality from abiotic factors (Harrington *et al.* 2001). In the case of multivoltine species, higher temperatures should, all other things being equal, allow faster development times, probably allowing for additional generations within a year (Ward & Masters 2007).

The knowledge of the **overwintering biology** and **cold tolerances** of potential invasive herbivores would provide a good indication of whether survival is possible in new locations (Bale & Walters 2001; Ward & Masters 2007). Unfortunately, such detailed information is lacking for the vast majority of potential invasive herbivore insects (Ward & Masters 2007). On the whole, non-indigenous species that are precluded by climate (for example, their propagules die or fail to reproduce) or whose ranges are restricted by climate, will survive and/or spread (Simberloff 2000) with more suitable temperatures. For example, Battisti *et al.* (2005) reported a latitudinal and altitudinal expansion of the pine processionary moth (*Thaumetopoea pityocampa*); over the past 32 years, *T pityocampa* has expanded 87 km at its northern range boundary in France and 110–230 m at its upper altitudinal boundary in Italy. By experimentally linking winter temperature, feeding activity and survival of *T. pityocampa* larvae, they attributed the expansions to increased winter survival due to a warming trend over the past three decades.

Moreover, there are evidences about **new invasions of migratory insects** as a consequence of rising temperatures. For example, Sparks *et al.* (2007) note that the number of species of migratory Lepidoptera (moths and butterflies) reported each year at a site in the South of the UK has been rising steadily. Authors found that this number is very strongly linked to rising temperatures in SW Europe and point out that further climate warming within Europe will increase the numbers of invasion of migratory Lepidoptera reaching the UK.

Most temperate species have some form of **winter diapause** (Ward & Masters 2007; Bale *et al.* 2002). In univoltine species, diapause is an obligatory part of the annual life cycle, whereas it is facultative in multivoltine species where diapause may be initiated in response to abiotic or biotic triggers (Ward & Masters 2007; Bale *et al.* 2002). The identity of these triggers may determine the response of an insect species to climate change (Ward & Masters 2007).

Non-diapausing, frost sensitive species and those which are able to overwinter in their active stages, show an increase of winter survival in warm winters. These species can be expected to increase population densities and expand their geographical ranges to higher altitudes and latitudes as average temperatures increase (Bale *et al.* 2002).

Through measuring, or taking from any existing literature, the relative growth rates and the diapause requirements of an assemblage of insect herbivores, Bale *et al.* (2002) presented a model based on the knowledge of insects growth rate and diapause requirements to define the response of insect species to warming. This framework can be applied to predict range expansion or contraction, which is a crucial factor for potentially invasive species (see Fig. 4).

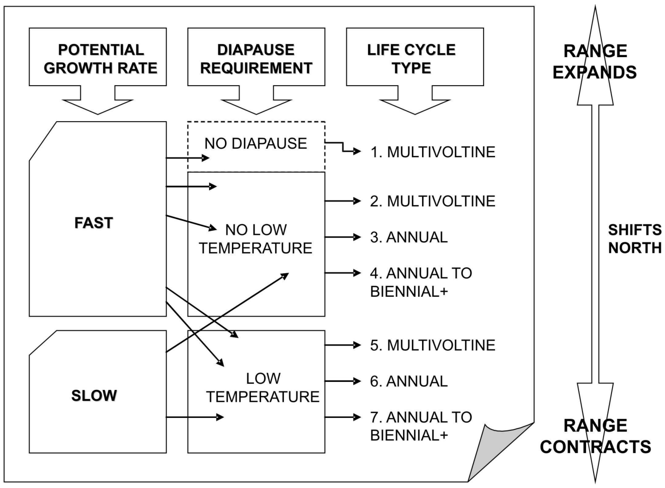

Fig. 4. Simplified model of insect response to environmental warming. (Modified from Bale *et al*. 2002)

The model predicts that fast growing, nondiapausing species (e.g. multivoltine), and those which do not have a low temperature requirement to induce diapause, will respond the most to increased temperatures and expand their ranges (Ward & Masters 2007). So, growth rate coupled with information on overwintering strategy may provide a pointer to future invasion success of a wide range of insect species (Ward & Masters 2007).

Nevertheless, no single trait provides a strong assessment of invasive risk. The use of several traits simultaneously may still provide good indications as to which species are likely to be positively affected by climate change and may thus have the potential to become invasive.

B. Propagule pressure

Propagule pressure is emerging as a single consistent correlate of the establishment success of non native species (Lockwood *et al*. 2005). Propagule pressure is a function of the frequency and number of propagules introduced into a habitat and it will be dependent on the dispersal abilities of the insect, the distance it has to travel, and the area of the habitat that it is invading. An increased number of introduction events may increase the likelihood that some propagules will arrive at a time when conditions are favourable to establishment (Lockwood *et al*. 2005; Ward & Masters 2007). The identity, origin and volume of introduced species arriving into an area may all alter substantially with climate change (Ward & Masters 2007).

Large-scale shifts in the geographical patterns of agricultural and forest production are expected because of climate change, and thus, **the origin of produce and its transport pathways** may change. This will allow a whole new collection of potential invaders to become associated with, and to make use of, each transport route (Bale & Walters 2001). In addition, it is possible that the invasibility of vulnerable agro-ecosystems to non-native species could alter as a result of changes in vegetation in response to a warmer and drier climate (Cannon 1998).

Changes in **atmospheric circulations patterns** could lead to **aerially dispersing insects** reaching new areas during times of the year that are more favourable to their establishment (Coulson *et al*. 2002). There are other meteorological factors that influence insect flight, especially wind speed and direction, rainfall, humidity and isolation, but too little is currently known as to how these may change in the future, and what their impact will be on insect flight, to warrant discussion (Bale *et al*. 2002).

It is clear that on average climate change will have a positive impact on propagule pressure and that we can expect many novel species to form a greatly enlarged pool of potential invaders (Bale & Walters 2001).

C. Changes in resource/niche availability

It is expected that the increase in **resource availability** (in terms of the quantity, structure and diversity of plant species) will also affect the invasion success of insect herbivores. Furthermore, climate change may itself influence resource availability through increased levels of disturbance and changes in species distribution (Bale & Walters 2001).

Levels of disturbance are greatly increased through extreme events such as landslides, intense storms, late frosts and severe drought. These are predicted to become more frequent in the future (Alcamo *et al*. 2007). The occurrence of such extreme climatic events may lead to detrimental effects and population crashes of native species (particularly where these are already close to their climatic tolerance limits). This is consistent with a reduction of levels of competitors and with an increase in available resources and it may provide a window within which successful invasions may occur (Ward & Masters 2007).

As well as more frequent extreme events, future climatic conditions are also expected to become more variable (IPCC 2001). This may give species the opportunity to become established for short periods of time in areas where normal conditions could be inappropriate. This may be of considerable concern in relation to pest species, which can cause severe damage over relatively short time scales (Ward & Masters 2007).

On the other hand, the departure of a species from a community, as its climatic tolerances are exceeded, could result in increased levels of resources becoming available (Ward & Masters 2007) and may provide opportunities for non-native species' establishment. Ward and Masters (2007) carried out a meta-analysis that suggests that niche availability in terms of plant structure (an increase in resource levels for insect herbivores) will increase under elevated CO_2 levels associated with climate change.

MARINE ENVIRONMENT

The spread of exotic species and climate change are one of the most serious threats to oceans. Despite considerable interest in predicting the spread and success of ''invasive'' species, few data are already available to assess whether climate change might facilitate invasions by favouring the introduction of non-indigenous species (Stachowicz *et al*. 2002b). Humans transport countless species around the world, and, although many of these introductions presumably fail because of unfriendly climate in the host region, global warming may relax this limitation (Stachowicz *et al*. 2002b).

The direct components of predicted climate change affecting marine organisms over the next century are: **(i)** temperature increase; **(ii)** sea level increase and subsequent changes in ocean circulation; and **(iii)** decrease in salinity (Harvell *et al*. 2002). Climatic change affects many ecological properties and it interacts with alien species in two ways, by: **1)** directly altering physical–chemical conditions (primarily temperature but also related oceanographic characteristics), and **2)** indirectly contributing to change the new communities patterns (Occhipinti-Ambrogi 2007).

Biological responses to abiotic changes associated with climate change are complex (see Figure 5). Climate change and specifically global warming can have a cascade of effects in the marine environment (Carlton 2001). Greenhouse gas emissions (mainly CO_2), together with increases in global mean temperature (consequently, a warming seawater), will result in a cascade of physical and chemical changes in marine ecosystems (Harley *et al.* 2006).

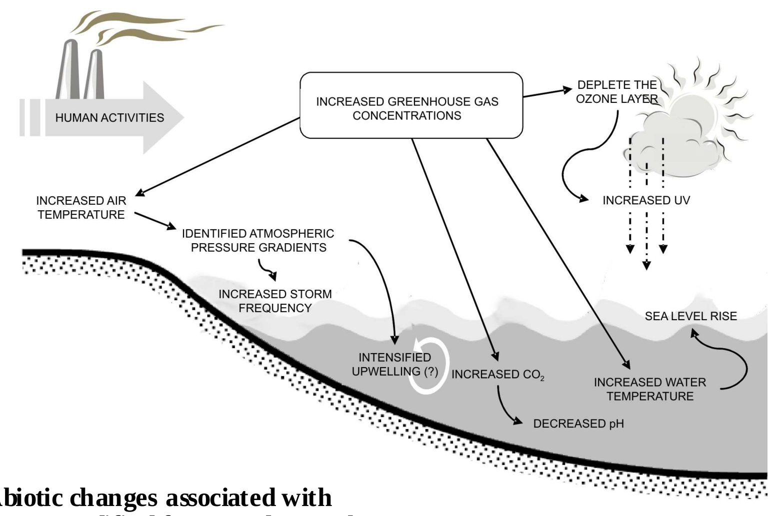

Figure 5. Abiotic changes associated with climate change. Modified from Harley *et al.*

The consequences of temperature change also include vertical stability of the water column and upwelling. Altered rainfall amounts could create new patterns of estuarine salinity dynamics, favouring particular euryhaline species (Carlton 2001). Changes in atmospheric circulation might also change storm frequency and precipitation patterns and alter circulation, and therefore **the dispersion pathways of alien species** (Occhipinti-Ambrogi 2007). Ocean circulation, which drives larval transport, will also change, with important consequences for population dynamics (Harley *et al*. 2006). Changing atmospheric conditions leading to altered ultraviolet light penetration or changing precipitation patterns can lead to altered patterns of primary production (e.g., by favouring species that are more efficient to get nutrients at different concentrations) (Carlton 2001). Altered rainfall amounts could also create new patterns of estuarine salinity dynamics (Carlton 2001).

Carlton (2001) summarizes the potential responses of biological invasions to the drivers of climate change in the oceans (Hobbs & Mooney 2005):

- Enhance invasions under warmer conditions (A): warmer-water alien species become more abundant where established and could expand their ranges to now-warmer higher latitudes. Invasions newly entering higher latitudes may interact with cold-adapted neo-genotypes of non-indigenous species, leading to their extinction (genetic swamping) or continued existence only in higher-latitude refuge.

- Enhance invasions under warmer conditions (B): Conversely, lower-latitude exotic populations may become extinct as waters become too warm, permitting new invasions of other warmer water or eurythermal taxa.

- Enhance or depress invasions under changing patterns of primary production, altered salinity regimes from changing precipitation patterns, and other changes: new primary trophodynamic regimes, new patterns and processes of estuarine oceanography (e.g. relative altered salinity dynamics, particularly the scale of horizontal intrusion of salt wedge), and other physicochemical conversions either enhance or depress new invasions.

Following the scheme by Harley *et al*. (2006) (see Figure 6), changes in the life cycle of a generic marine species need to be considered first.

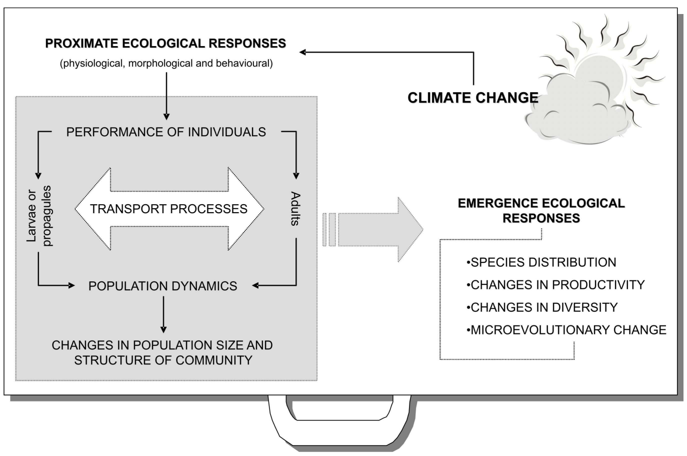

Figure 6. Potential ecological responses to climate change. The ecological effects of global climatic change include shifts in the performance of individuals, the dynamics of populations and the structure of communities.
Modified from Harley *et al.* (2006) and Occhipinti-Ambrogi (2007).

Thus, the effects of climatic change described in figure 5 lead to ‘‘emergent’’ patterns such as changes in species distributions, biodiversity, productivity and microevolutionary processes, that are connected with the effects of the introduction of alien species, especially if they have a dominant or prevalent population in the new environment (Harley *et al*. 2006; Occhipinti-Ambrogi 2007).

Climate change will play a role in determining **the rate at which new species are added to communities** (Harley *et al*. 2006). The most commonly predicted effect of global ocean warming is a **poleward shift in the distribution boundaries of species with an associated replacement of cold water species by warm water species** (Occhipinti-Ambrogi 2007). Warming temperatures can facilitate the establishment and spread of intentionally or accidentally introduced non indigenous species (Carlton 2000; Stachowicz *et al.* 2002b).

- For example, by the 1950s the sudden increase in populations of *Saurida undosquamis* and *Upeneus moluccensis* was attributed to a rise of 1.0-1.5 ºC in sea temperature during the winter months of 1954-1955 (Galil 2007). The Erythrean invasion has accelerated in recent years, with increasing records of newly discovered Erythrean species and expansion towards other areas of the Mediterranean Sea. If global warming were to affect the Mediterranean Sea water temperature, then tropical invasive species would gain a distinct advantage over the native fauna (Galil & Zenetos 2002).

- Another example is the dramatic and continuous spread of *Caulerpa racemosa* throughout most of the Mediterranean Sea and the Atlantic Ocean (Occhipinti-Ambrogi 2007); the growth rate of this species is correlated with favourable characteristics for its development and a mild climate (Ruitton *et al*. 2005).

- Bañón *et al*. (2002) contribute with four new citations of fishes recorded in the last few years in Galician waters (Northwest of Spain): *Physiculus dalwigkii*, *Neoscopelus microchir*, *Pisodonophis semicinctus* and *Gaidropsarus granti*. The fact that Atlantic species as *Pisodonophis semicinctus* and *Gaidropsarus granti* were previously recorded in the Mediterranean Sea, where they were unknown, and are now found in Galician waters, represents a new northern limit for their distribution in the North-east Atlantic and seems to indicate a gradual displacement of these species northwards, using the Gibraltar Strait as an escape valve in these transports to the north. Additionally, in the Mediterranean as well as in the European Atlantic Sea, this phenomenon has increased rapidly in the last ten years (Bañón *et al*. 2002). Other example is the arrival of *Seriola rivoliana* (a tropical fish) to European Atlantic waters, as its appearance is related to the increasing water temperature (Quéro *et al*. 1998).

More generally, climatically driven **changes in** species composition and abundance will alter species diversity, with implications for ecosystem function as well as productivity and **invasion resistance** (Stachowicz *et al*. 2002a; Harley *et al.* 2006).

Climatic driven changes may affect both **local dispersal mechanisms**, due to the alteration of current patterns, and **competitive interactions between alien and native species**, due to the onset of new thermal optima and/or different carbonate chemistry. The magnitude and variety of climatically forced changes in the physical environment will provoke responses in the biosphere thus altering the balance of native species versus non-indigenous species, via changes in population size and effect of interacting species (Occhipinti-Ambrogi 2007).

Species that are amenable to **ENSO** (El Niño-Southern Oscillation phenomena) transport, could be a possible pool of candidate species that are likely to either gradually shift North with global climate change, or establish permanent populations (when they could not before) if transported north by ENSO phenomena (Carlton 2001).

The effects of warming climate are a cause for physiological stress (which acts more strongly on species already close to their tolerance limit). Anomalous temperature stress can cause mass mortalities in benthic organisms that lead to **empty niches,** which **can be used** (and therefore colonised) **for new non-indigenous species** (Occhipinti-Ambrogi 2007). So, if certain taxa become less abundant they may create further opportunities, due to their population declines, for new invaders if the former occupied unique trophic positions or unique microhabitats (Carlton 2001).

The competition for open space on the substrate is heavily influenced by the **timing of recruitment**, and this in turn is highly dependent on temperature. Changing seasonal patterns of temperature may favour **the settlement of invasive species in a particular time of the year**, and long lasting consequences in preventing the recruitment of native species later (Occhipinti-Ambrogi 2007). Stachowicz *et al*. (2002) demonstrated that the recruitment pattern of the three introduced species of ascidian (*Botrylloides violaceous*, *Diplosoma listerianum*, and *Ascidiella aspersa*) coincided with a period of low recruitment of other native species of ascidians; the timing of the initiation of recruitment was strongly negatively correlated with winter water temperature, indicating that invaders arrived earlier in the season in years with warmer winters. The recruitment of non-indigenous species during the following summer was also positively correlated with winter water temperature. On the contrary, the magnitude of native ascidian recruitment was negatively correlated with winter temperature. Authors suggest that the greatest effects of climate change on biotic communities may be due to changing maximum and minimum temperatures rather than annual means (Stachowicz *et al.* 2002).

Increased ocean temperature also causes **pathogen range expansions**. The negative effects of disease are likely to become more severe, as pathogens are generally favoured by warmer temperatures relative to their hosts (Harvell *et al*. 2002; Harley *et al*. 2006). Harvell (2002) provides an example of three coral pathogens (e.g. *Aspergillus sydowii*) that grow well at temperatures close to or exceeding probable host optima, which suggests that they would increase in warmer seas. Moreover, the author collects some citations about the positive correlations between growth rates of marine bacteria and fungi with temperature. Among marine invertebrates and eelgrass, many epizootics of unidentified pathogens are linked to temperature increases, but the mechanisms for pathogenesis are unknown (Harvell *et al*. 2002).

Carlton (2001) proposes **two predictions** that arise from the phenomenon of warming trends in middle to higher-latitude ocean waters: 1) previously lower latitude-restricted species will colonise higher latitudes for the first time, and 2) there will be an increase in abundance of species of evolutionarily warmer water affinity.

Carlton (2001) points out **two additional critical components** of the response of marine biota to climate change: 1) whether, as might be expected, there are corresponding and simultaneous southern contractions of taxa that appear to be moving further North (e.g. the northern range of *Littorina littorea* has expanded while its southern range has contracted, and 2) whether native taxa are responding to climate change as well by moving North (and contracting South) and becoming invaders as well. Documentation of such patterns will be essential to determine if biogeographical shifts are now occurring in the native as well as the introduced biota.

INFECTIOUS DISEASE AGENTS AND CLIMATE CHANGE

Climate-linked invasions might also involve the immigration of unwanted neighbours such as pathogens or diseases (Walther *et al*. 2002).

Epstein et al. (1998) have showed that, according to the World Health Organization (1996), thirty new diseases have emerged in the past twenty years, and there are resurgence and a redistribution of old diseases on a global scale like malaria and dengue fever, both vectored by mosquitoes.

Epstein *et al.* (1998) also examined recent evidences that indicate upward movements in disease carrying insects, and point out that **vector-borne diseases** (e.g., involving insects and snails as carriers) could shift their range in response to climate change (Leaf 1989; Shope 1991; Patz *et al*. 1996; McMichael *et al*. 1996; Carcavallo *et al*. 1996: in Epstein *et al*. 1998).

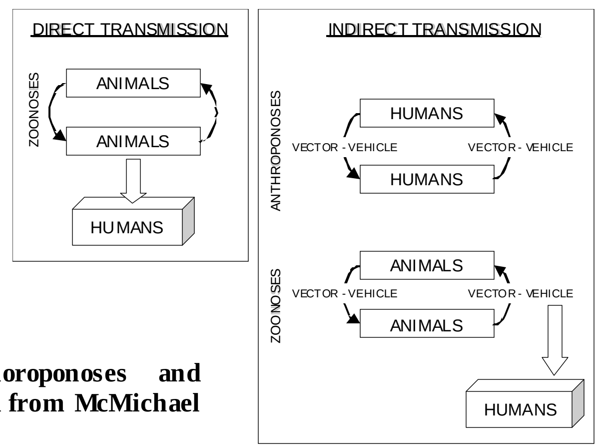

Figure 7. Anthoroponoses and zoonoses. Modified from McMichael *et al.* 1996.

On the whole, based on the mode of transmission (see figure 7), infectious diseases can be classified into two categories: those that spread directly from person to person (through direct contact or droplet exposure) and those spreading indirectly through an intervening vector organism (mosquito or tick) or a non-biological physical vehicle (soil or water) (McMichael *et al*. 1996). The most important vector-borne diseases in Europe are malaria and Lyme disease, which are transmitted by mosquitoes and ticks, respectively (Githeko *et al*. 2000).

Infectious diseases also may be classified by their natural reservoir: anthroponoses (human reservoir) or zoonoses (animal reservoir) (McMichael *et al*. 1996).

Several possible transmission components include pathogen (viral, bacterial, etc.), vector (mosquito, tick, snail, etc.), non-biological physical vehicle (water, soil, etc.), non-human reservoir (mice, deer, etc.) and human host. These diseases are highly susceptible to a combination of ecological and climatic factors because of the numerous components in the transmission cycle, and their interaction with the external environment (McMichael *et al*. 1996).

If climate change affects one or more components in the transmission cycle of diseases (the pathogen, biological vector and/or animal reservoir) it could be possible that diseases increase their range.

Infectious disease agents often are invasive alien species, such as, *Aedes albopictus, Aedes aegypti, Vibrio cholera*, etc., and there is evidence linking the impact of these invasive species and climate change. Many vectors, accompanying the increase of temperatures, are likely to expand their ranges within Europe, and new vector species may be introduced from the tropics (Githeko *et al.* 2000).

Some cholera epidemics appear to be directly associated with ballast water (IMO 2002). *Vibrio cholerae* resides in marine ecosystems by attaching to zooplankton, and the survival of these small crustaceans in turn depends on the abundance of their food supply, phytoplankton (McMichael *et al.* 1996). Phytoplankton populations tend to increase (bloom) when ocean temperatures are warm (McMichael *et al.* 1996). Ocean currents sweeping along coastal areas translocate plankton and their bacterial passengers (Colwell 1996). As a result of these ecological relationships, cholera outbreaks occur when ocean surface temperatures rise (Colwell 1996). Furthermore, pathogenic *V. cholerae* could grow in water with low salinity if the water temperature is relatively high and organic nutrients are present in high concentrations (Colwell 1996).

Mosquitoes are highly sensitive to climatic factors. For example, *Anopheline* spp. & *Aedes aegypti* mosquitoes have established temperature threshold for survival, and there are temperature-dependent incubation periods for the parasites and viruses within them (extrinsic incubation period –EIP-). Warmer temperatures (with sufficient moisture) could increase mosquito populations, biting rates, mosquito activity and abundance, and decrease the duration of EIP (Epstein 1998). This fact leads us to think that if climate changes benefits the survival of this kind of vectors, diseases (like malaria or dengue, for example) will have more opportunities to arrive and spread in new locations. For example, Githeko *et al.* (2000) point out that *Aedes albopictus* (a major vector of dengue fever) has spread to 22 northern provinces in Italy since being introduced eight years ago (Romi *et al.* 1999). The West Nile virus caused outbreaks in France in the 1960s and in Romania in 1996. Occasional outbreaks of malaria in Europe arise when infective mosquitoes are imported from the tropics by aircraft - for example, since 1969, there have been 60 such cases reported from a number of European countries (Danis *et al.* 1999, in Githeko *et al.* 2000).

Cumming & Van Vuuren (2006) call for attention on the potential impact of climate change on tick-borne diseases because of their extremely high medical and economic importance for humans and livestock. Under different climate change conditions, these authors explored the current and future invasive potential of 73 African tick species to other locations. Results show that under all projected scenarios (over the next 100 years), climatic conditions are likely to become more suitable in Africa as well in the rest of the world, predicting an average increase in global habitat suitability of 1-9 million km^2. Such greater habitat suitability within Africa implies: **1)** an increase in tick population sizes also in areas that are currently marginal, and **2)** a higher risk of transfer to the rest of the world through animal trade. Tick community composition will also be affected depending on the severity of climate change, influencing, as a consequence, tick-borne pathogens and patterns of transmission with significant impacts for human and animal health.

Although a similar trend for non-African ticks is only presumably expected, more concern should be paid to Europe, where the expansion of tick-borne diseases and tick species ranges increased in recent decades (Den Boon *et al.* 2004; EEA 2004).

It is clear that invasive alien species are linked to humans, animals and plants diseases. If climate change affects these species providing new suitability chances in new locations, the incidence of these diseases could increase.

So, we need to keep in mind human health (and of course animal and plant health) when we deal with biological invasions and climate change.

CONCLUSIONS AND RECOMMENDATIONS

- The risk posed by Invasive Alien Species under climate change conditions is in general underestimated because models and scenarios, mainly focused on native biodiversity, have poorly explored the issue.

- Invasive alien species are already a problem by causing biodiversity and economic losses as well as problems to human, animal and plant health. "As invasive species and climate change are considered two of the three main threats to biodiversity, the two operating together could be expected to produce extreme outcomes" (Low 2008).

- Current biotic changes caused by invasive alien species could further interact with climate change increasing ecosystems' vulnerability and therefore the risk of new invasions. Once invasive alien species become established in large numbers, their consequences are often irreversible. Under climate change conditions, invasions can be produced by a) alien species introduced *ex novo*, b) already established invasive alien species (spread), and c) already established invasive alien species non invasive at present but becoming invasive under new ecological conditions

- Climate change could alter the structure and composition of native communities and, as a consequence, the way an ecosystem functions, increasing the risk of biological invasion. It is also likely to increase the potential distribution and abundance of IAS, further enlarging areas at risk of invasion, and threatening the viability of current management strategies against IAS. The identification of new potential areas of invasion is a key tool to anticipate large-scale and long-term effects of invasive alien species. Studies identifying potential new suitable areas for invaders should be considered in policies on the introduction of exotic species, prevention of new infestations and management of IAS already established.

- There is a lack of knowledge on the biology of IAS and how their populations respond to climate change so it is necessary to make an effort in order to improve information. However, this is no reason to postpone action to avoid a current problem that is very likely to increase in magnitude in the future due to climate change.

- It is necessary to consider human health as well as animal and plant health when dealing with biological invasions and climate change.

- It is difficult to predict how climate change will affect invasive processes *per se* as well as in combination with other factors of global change (biotic changes, land use changes, etc.). There is a need for more research on biological invasions linked to climate changes. The influence of dispersal, propagule pressure and species interactions should be included into future research projects on biological invasions linked to climate change. Other key issues for future research projects are:

  - the identification of key demographic transitions that influence populations dynamics;
  - the prediction of changes in the community-level impacts of ecologically dominant species;
  - the populations' ability to adapt, and the scales over which climate will change and living systems will respond;
  - the synergistic effects between climate and other anthropogenic variables (e. g. land use, fishing pressure, etc.) that likely exacerbate the abundance and impact of IAS;
  - predictive models.

- In this framework, strengthening IAS policies in order to reduce current and potential biotic changes driven by IAS that could interact with climate change is a must.

- Policies to halt biological invasions should be strongly based on prevention. Such measures have to be developed and set up with urgency because any procrastination increases the chance of new invasions.

- Under the precautionary approach any intentional introduction of alien species (e.g. plants proposed as biofuel crops) should be conditioned to exhaustive risk analysis processes which have to be reinforced by including considerations related to climate change. Likewise risk analysis on pathway and vectors should take into account potential interactions with climate change to prevent unintentional introductions. Therefore research and improvement of predictive models is highly desirable.

- The potential effects of climate change on the potential distribution and abundance of IAS highlight the desirability of considering the effects of altered climate and atmospheric chemistry when undertaking risk analysis for biotic invaders.

- Native species that are likely to go extinct under climate change have been the main object of concern among scientist, governments and international institutions/organizations. On the contrary very few attentions have been paid to what will replace them. Public awareness campaigns on climate change should include invasive alien species as a part of the problem and stakeholders should be engaged in the debate to develop codes of good practice (see the European Strategy on Invasive Alien Species) (Genovesi & Shine 2004), in order to reinforce policies of prevention under the leadership of governments.

- Setting in motion early warning systems constitutes another must. Pest detection and inspection capacities should be implemented. Surveillance programmes are critical if prevention fails. Rapid response capability should be enhanced to avoid the spread of IAS once they have entered a new territory.

- Also mitigation of already established IAS should be carried out, giving priority to silent populations of IAS which are unable to expand because of unsuitable conditions (e.g. temperature), or that could increase as a result of extreme events, and/or problematic species such invasive alien flammable plants.

- The implementation of such measures should be carried out taking into account the bio-geographical approach instead of the country approach. This is particularly important due to species' potential shift ranges under changing climate, and special caution (case-by-case approach) should be put when considering species' self-expansion from adjacent regions to areas where they are not native in response to human induced climate change.

- Last but not least, the restoration of degraded ecosystems and the reduction of other environmental threats (e.g. contamination, natural resources over-exploitation, etc.) should be promoted in order to increase ecosystem resilience.

- Biological invasions are already a problem which is very likely increased under climate change. While tools to fight IAS already exist, countries' concern is still scarce and action is urgent.

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