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PAPER



Palms tracking climate change

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ABSTRACT

Aim Many species are currently expanding their ranges in response to climate change, but the mechanisms underlying these range expansions are in many cases poorly understood. In this paper we explore potential climatic factors governing the recent establishment of new palm populations far to the north of any other viable palm population in the world.

Location Southern Switzerland, Europe, Asia and the world.

Methods We identified ecological threshold values for the target species, *Trachycarpus fortunei*, based on gridded climate data, altitude and distributional records from the native range and applied them to the introduced range using local field monitoring and measured meteorological data as well as a bioclimatic model.

Results We identified a strong relationship between minimum winter temperatures, influenced by growing season length and the distribution of the palm in its native range. Recent climate change strongly coincides with the palm's recent spread into southern Switzerland, which is in concert with the expansion of the global range of palms across various continents.

Main conclusions Our results strongly suggest that the expansion of palms into (semi-)natural forests is driven by changes in winter temperature and growing season length and not by delayed population expansion. This implies that this rapid expansion is likely to continue in the future under a warming climate. Palms in general, and *T. fortunei* in particular, are significant bioindicators across continents for present-day climate change and reflect a global signal towards warmer conditions.

Keywords

Arecaceae, biogeography, bioindicator, exotic species, global warming, invasion, northernmost palm population, Ticino, *Trachycarpus fortunei*, vegetation shift.

INTRODUCTION

In recent years, and as a result of recent climate warming, changes in the behaviour and distribution of species, the composition of communities and interactions within them, and the structure and dynamics of ecosystems have been observed in an array of habitats from the poles to the equatorial regions (e.g. Hughes, 2000; Walther *et al.*, 2002; Parmesan & Yohe, 2003; Root *et al.*, 2003). Plants, for example, are responding to the enhanced warming of recent decades by changing their phenological patterns and/or shifting their ranges to higher latitudes or altitudes (Walther, 2004). Furthermore, evidence is arising that not only are indigenous species responding to changing environmental conditions, but introduced species may also be profiting from these

changing conditions (Walther, 2000; Sobrino Vesperinas *et al.*, 2001; see also Dukes & Mooney, 1999; Simberloff, 2000). At the southern foot of the Alps, among the assemblage of invading evergreen broad-leaved plants, an introduced palm species [*Trachycarpus fortunei* (Hook.) Wendl.] has successfully colonized deciduous forests and established a vigorous population that already has fertile individuals (Gianoni *et al.*, 1988; Carraro *et al.*, 1999; Walther, 2003).

In the palaeobotanical literature, palms in general are recognized as effective bioindicators of warm climates. The presence of fossil palm remains in the geological record is invariably interpreted as indicative of warm and humid climatic conditions during the formation of the particular geological stratum (e.g. Mai, 1995).

Under current global climates, palms reach their greatest proliferation in the tropics and are much less prominent and diverse

in temperate regions (Good, 1953; Jones, 1995; Gibbons, 2003; Löttschert, 2006). However, in recent years evidence is increasing that the most cold-hardy palm species are occurring beyond the usual latitudinal range limit of palms (Stähler, 2000; Walther, 2002a; Francko, 2003). Here, we compile and synthesize the various recent records reporting new occurrences of palms outside the known range of global palm distribution, focusing on the hemp palm, *T. fortunei*, the most widely cultivated species at the latitudinal palm range margin. We explore potential climatic factors governing the recent establishment of a new sub-spontaneous palm population in southern Switzerland, far to the north of any other viable palm population in the world. Based on gridded climate data, altitude and distributional records from China, i.e. the native habitat of *T. fortunei*, we aim to identify the limiting climatic parameters in the native range and to verify whether a shift in climate might explain the palm's recent spread in the introduced range south of the European Alps using a bioclimatic model. These findings are then applied on the global scale in order to assess whether there is an observed coherent range expansion of this species on various continents which can then be interpreted as a global signal of the shifting of the climate towards warmer conditions.

MATERIALS AND METHODS

The native habitat of *T. fortunei* is located in south-eastern Asia (Delectis Florae Reipublicae Popularis Sinicae, 1991; Wu & Ding, 1999; Gibbons, 2003), as shown in Fig. 1.

Based on the distribution of this particular palm species in its native range (Delectis Florae Reipublicae Popularis Sinicae, 1991;

Wu & Ding, 1999), we derived the species' specific climatic requirements with regard to temperature and water availability. Whereas the absolute value of low temperatures limiting the species' survival has been studied intensively (Winter, 1976; Larcher & Winter, 1981; Sakai & Larcher, 1987; cf. also Walther, 2002a), experience from field experiments suggests that at least two climatic factors, i.e. low temperatures in winter and length of the growing season, are involved in limiting this species' northern/upper distribution when exposed to natural conditions in the field (Walther, 2003; see also Fitzroya, 2004).

In this study we applied two approaches for deriving climatic constraints to the species' distribution in its native range. Both approaches used monthly climate data from the Climatic Research Unit, University of East Anglia (CRU data set) (0.5°; New *et al.*, 2000) averaged over the period 1961–90.

First, we superimposed gridded data of minimum monthly temperatures and growing season length [growing degree days above 5 °C (GDD₅) per year] on the distribution map of *T. fortunei* in its native range in China in order to define the species' limits with regard to these two bioclimatic variables. Information on local altitudinal limits (Delectis Florae Reipublicae Popularis Sinicae, 1991; Wu & Ding, 1999) was used to exclude those grid cells within the range of the species but where the reference altitude was higher than the known upper elevational limit of locally occurring individuals of *Trachycarpus*. The resulting two subsets of grid cells separate grid cells whose geographical position (latitude/longitude) or reference altitude in the gridded climate data set is outside the range of *T. fortunei* occurrences from those that overlap with the range of *T. fortunei*. The difference in climate between these two subsets was used to define the potential

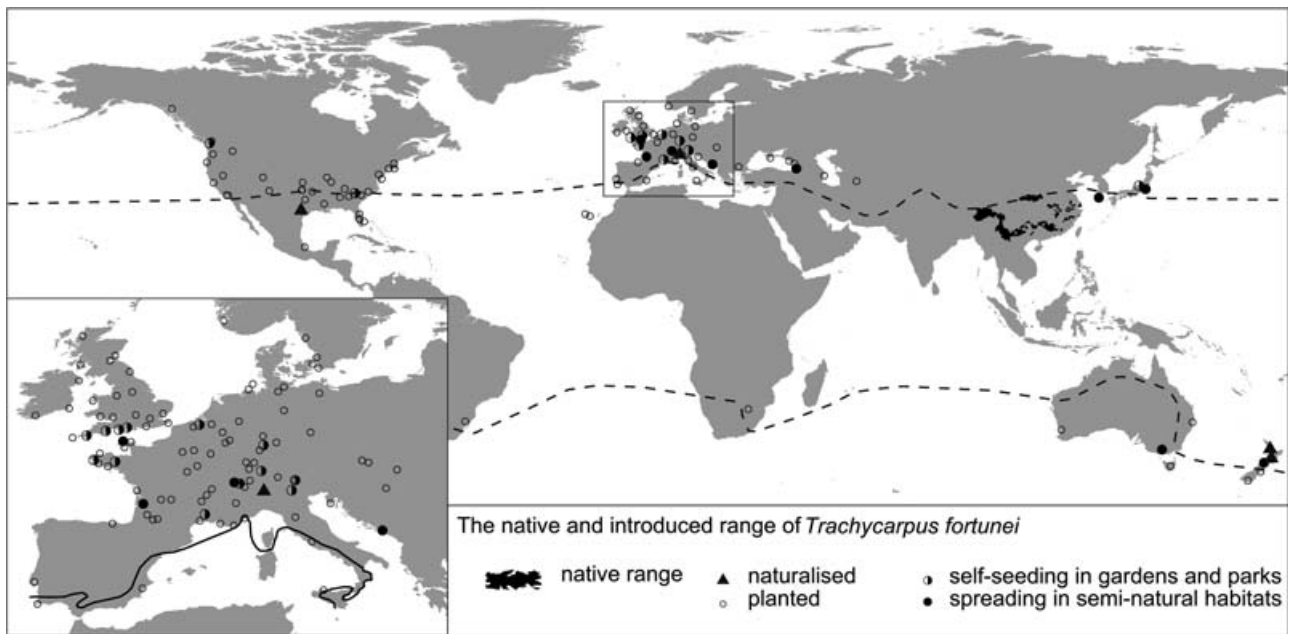


Figure 1 The native range of *Trachycarpus fortunei* in China and a compilation of sites where *T. fortunei* occurs outside its native range. The broken lines indicate the poleward range margins of global natural palm distribution. In the inset, the solid line shows the northernmost palm population (*Chamaerops humilis*). The symbols represent a (non-exhaustive) compilation of *Trachycarpus* sites based upon literature and Internet searches as well as personal observations and contacts; for details see text, Acknowledgements and Supplementary Appendix S4.

range, especially towards colder areas (cf. Beerling *et al.*, 1995; Edwards *et al.*, 1998; Guisan & Thuiller, 2005).

Secondly, although we focus here on the northern/upper limit of palm ranges, an estimate of the complete bioclimatic envelope of this species was derived by comparing the realized and the modelled distribution in the native range, using the bioclimatic model STASH (STAtic SHell; cf. Sykes *et al.*, 1996), based on gridded climate data derived from the CRU data set for the period 1961–90. This temporal envelope compares well with the available plant distribution data for its native habitat (Delectis Florae Reipublicae Popularis Sinicae, 1991). The STASH bioclimatic model is a simple model that uses a minimum set of bioclimatic parameters (mean temperature of the coldest month, growing season warmth, a drought index and for some species a requirement for chilling before budburst in the spring) to describe a species' range. These parameters are assumed to present responses to important physiological mechanisms within a plant; for example, growing season length (growing degree days) is an index of the presence of energy suitable for the completion of a plant's life cycle. Some of these parameters act as on–off switches, if, for example, the mean coldest month temperature (which is a surrogate for the absolute minimum; Prentice *et al.*, 1992) in a grid cell falls below the species' minimum limit, that species is excluded from that cell. Other parameters act directly upon net assimilation and respiration and thus on growth rate, which is reflected as the degree of establishment success in a grid cell (see Sykes *et al.*, 1996, for full details).

For the introduced range, we then analysed local and regional meteorological measurements in order to verify whether critical climatic limits have been exceeded since *T. fortunei* started to expand its range into native vegetation in Europe. For the regional analysis, STASH was applied with the bioclimatic limits derived for the species' native range, using gridded climate data averaged over two different time periods (1931–60 and 1991–2000) for Europe (Mitchell *et al.*, 2004; 0.16° resolution). The first period was before the enhanced spread of palms and the second is well within the period of establishment and naturalization of *T. fortunei* in southern Switzerland. Thus, we are able to verify whether the invasion history documented with field reports in southern Switzerland is also reflected in the temporal pattern of changes in climatic conditions (cf. Dukes & Mooney, 1999; Walther, 2000) or is simply a chorological phenomenon, depending on the availability of seed sources and suitable habitats. The improved knowledge of the history, chronology and driving mechanisms of the observed local establishment of *Trachycarpus* populations south of the Alps was then used as a basis for a better understanding and interpretation of recent occurrences and shifts of *Trachycarpus* and other palm species at their poleward fringe area on the global scale.

RESULTS

Bioclimatic preferences in the native habitat

Two important bioclimatic factors exclude *T. fortunei* in China from higher latitudes and altitudes (Fig. 2). Our results show that

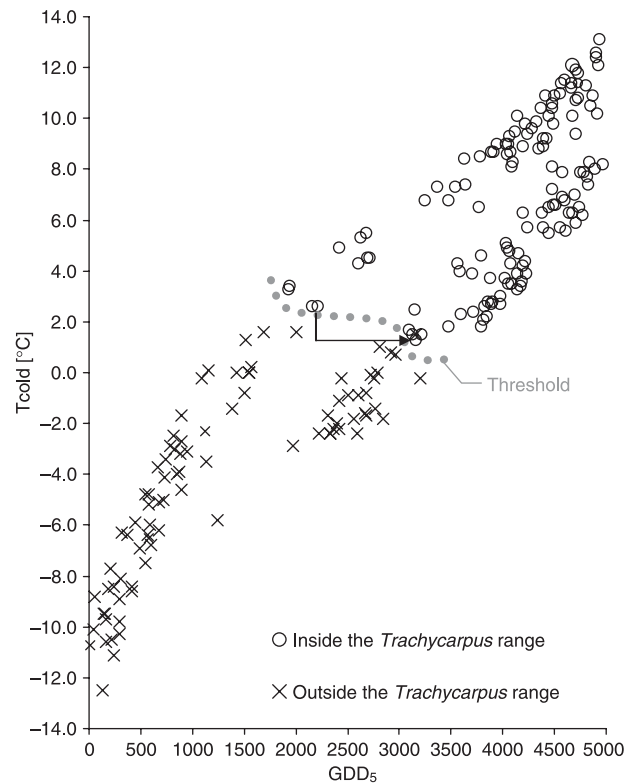


Figure 2 Bioclimatic limits of the distribution of *Trachycarpus fortunei* towards northern and upper range margins in the native habitat in China. (T_{cold} = monthly mean temperature of the coldest month; GDD_5 = growing degree days above 5 °C per year). The arrow indicates a compensatory effect of optimal growth in the growing season for unfavourable winter temperatures (for details see text).

a mean temperature of +2.2 °C is the threshold for the coldest month in areas with values of about 2300 GDD_5 . Assuming a global, generally applicable relationship between monthly mean temperatures and daily extremes (Prentice *et al.*, 1992), this corresponds to a minimum temperature of around –19 °C. In areas with values of significantly more than 3000 GDD_5 , the threshold temperature of the coldest month may be lowered by about half a degree (Fig. 2), which suggests a compensatory effect of unfavourable winter temperatures by optimal growth in the growing season.

In accordance with the analysis above, the STASH simulations achieved the best match with the observed distribution, using 2.2 °C as the lower limit of the monthly mean temperature of the coldest month and $GDD_5 = 2300$, when the southern/lower limit of the species distribution was defined by a maximum mean temperature of the coldest month of 15.5 °C and a tolerated drought index [defined by $1 - (AET/PET)$, where AET is actual evapotranspiration and PET is potential evapotranspiration; for details see Sykes *et al.*, 1996] of 0.26 (see Appendix S1 in Supplementary Material).

Potential and realized distribution in the introduced range

Numerous local floristic inventories, dating as far back as the nineteenth century, provided data for a detailed reconstruction

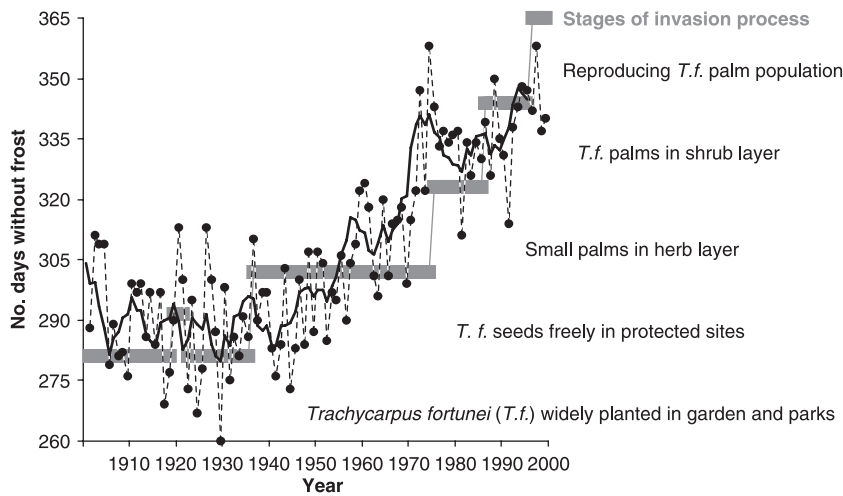


Figure 3 Local climate data vs. invasion history of *Trachycarpus fortunei* palms in southern Switzerland. Milder winters [here indicated by the number of days without frost per year; annual values (broken line and dots) and smoothed 5-year averages (solid line) are shown (data from Walther 2002b, modified)] are considered a key factor for the survival and establishment of reproducing palm populations. The later stages of the invasion process have only been reached in the period of warmer climatic conditions (for details see Supplementary Appendix S2 and text).

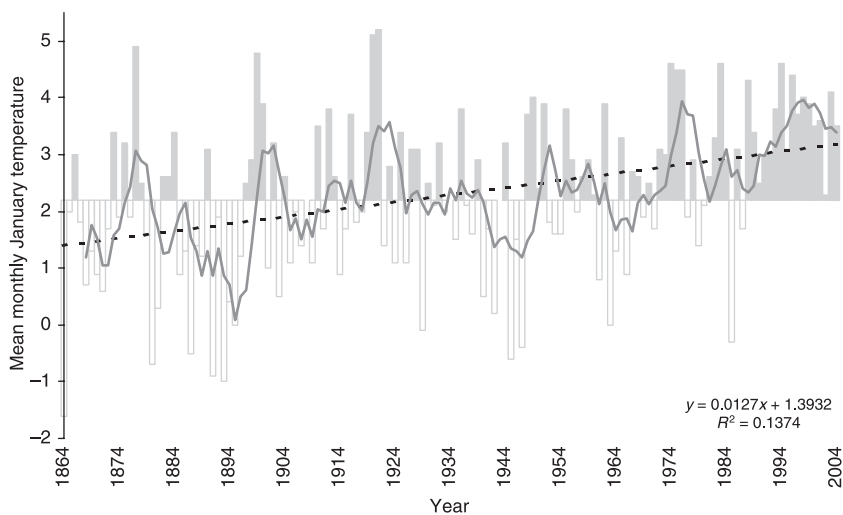


Figure 4 Annual values for mean monthly temperature in January from 1864 to 2004 (data from SMA MeteoSwiss: www.meteoschweiz.ch/web/de/klima/klimaentwicklung/homogene_reihen.html, Meteorological Station of Lugano; Begert *et al.* 2005). In addition, the linear trendline (dashed line) as well as smoothed values for 5-year averages (solid line) are shown.

of the chronology of spread and establishment of a new local palm population south of the Alps (see Appendix S2 in Supplementary Material). As in the case for many other ornamental species of the same origin, this palm was introduced to Europe in the late 18th/early 19th century (Jacobi, 1998). However, whereas the introduction and subsequent frequent cultivation in gardens and parks took place about two centuries ago and led to the establishment of large garden populations with fruiting individuals, it was only in the 1950s that the palm first succeeded in colonizing protected sites such as shady and humid gorges. Some 20 years later, in the 1970s, the first occurrences of palm seedlings in forest stands were documented; these seedlings persisted in the face of competition from the local indigenous flora and reached a fertile stage, so that substantial, fully functioning palm populations were thus established (Fig. 3; see also Appendices S2 & S3 in Supplementary Material).

With our knowledge of the species' specific climatic requirements in its native habitat (Fig. 2) and measured climate data for the introduced range we can now address whether the history of the spatio-temporal spread of *T. fortunei* does follow the pattern

of improving climatic conditions in the introduced range (Fig. 4).

Measured local meteorological data (Fig. 4) show that the periods with temperatures above the threshold value of a mean January temperature of +2.2 °C (Fig. 2) have obviously increased in length and frequency. The smoothed 5-year averages reveal that isolated occasional short-term events with favourable conditions before the 1950s developed into frequent short-term favourable events in the early second half of the 20th century, and finally into continuously favourable conditions from the mid-1980s (Fig. 4).

Furthermore, distinct differences can be seen in the simulated range for *T. fortunei* in Europe for the periods 1931–60 and 1991–2000, using the STASH bioclimatic model (Fig. 5). There is an obvious shift in the spatial distribution of *T. fortunei* in southern-central Europe. In particular, the range of suitable habitats was moving into the area of southern Switzerland during this time (see insets in Fig. 5). Whereas in the first period the conditions in southern Switzerland were not suitable for allowing enhanced growth and establishment of sub-spontaneous

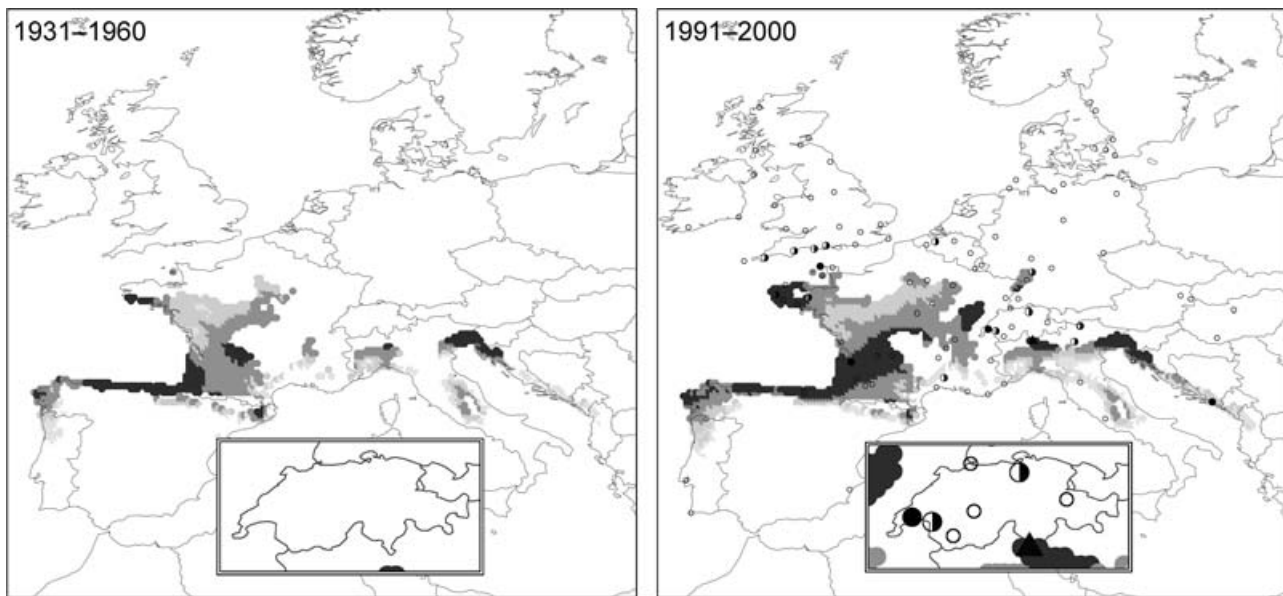


Figure 5 Simulated range for *Trachycarpus fortunei* in Europe for two different periods, based on species-specific bioclimatic limits in the native range. Dark shades of grey denote better conditions for establishment and growth (within the climatic envelope) than light shades due to the direct effect of climate on net assimilation and respiration simulated by the model (Sykes *et al.*, 1996). The insets show that in southern Switzerland the conditions became suitable for *Trachycarpus* palms only in the latter period. For symbol legend see Fig. 1.

populations (Fig. 5, left), in the latter period the area where *T. fortunei* has naturalized (southern Ticino/Switzerland) now overlaps with the simulated range of optimal bioclimatic conditions (Fig. 5, right).

The model output also suggests other areas in central Europe (e.g. coastal areas on the Bay of Biscay, but also new areas in central-western France and at the French–German border) where the conditions from a bioclimatic perspective seem to be becoming increasingly suitable for the growth of *Trachycarpus* (cf. also Fig. 1).

The new northernmost palm population from a global perspective

With this improved understanding of the history, chronology and driving mechanisms of an observed local establishment of palm populations in the introduced range (Appendix S2; cf. also Carraro *et al.*, 1999; Walther, 2002b, 2003), we are able to analyse and extrapolate these findings to the continental and global perspective.

The new sub-spontaneous population at the southern foot of the Alps is clearly located outside the known global distribution of palms (Fig. 1). This new exclave of palm distribution occurs c. 300 km north-northeast beyond the northernmost palm limit as recognized up to now (inset of Fig. 1), and its spatio-temporal development strongly suggests climate change to be an explanation for this (see above).

Occurrences of *Trachycarpus* north of the Alps in central Europe and on the southern coast of the British Isles can be seen as early stage invasions, where the seeds from planted *Trachycarpus* palms have been able to germinate in gardens and parks and to

survive at least for some limited time (see Fig. 1). On other continents, but still within the belt of global palm distribution, *T. fortunei* has been observed to spread out from garden areas into (semi-)natural habitats such as woodlands. Locally well-established plants have been reported, for example, from Austin/Texas (L. Lockett, pers. comm.) and from the North Island of New Zealand (e.g. Healy & Edgar, 1980) (Fig. 1).

DISCUSSION

It is widely accepted that a distribution including higher latitudes and altitudes of evergreen broad-leaved species in general, and palms in particular, is limited by the climatic conditions during the cold season (Woodward, 1987; Jones, 1995; Walther, 2002b, Francko, 2003; Lötschert, 2006). For the palm *T. fortunei*, a threshold mean temperature of the coldest month of about +2.2 °C was identified in its native range in China. However, enhanced growing degree accumulations of more than 3000 degree days may compensate for unfavourable winter conditions with temperatures down to about +1.3 °C. There is observational evidence from areas outside the native range with suboptimal conditions for the ecological interpretation of such compensatory effects (e.g. Walther, 2003; Fitzroya, 2004). Exposure of planted *Trachycarpus* palms to sub-lethal temperatures results in damage to fronds and spears and/or defoliation. As a consequence, a minimum growing degree day accumulation is required for the palm to recover from the damage and resume growth (Fitzroya, 2004). If that minimum is not achieved in one growing season, the plant is unable to fully replace damaged tissue, expends stored energy to replace greater lost mass at the cost of growth, and

enters a period of decline (Fitzroya, 2004). This observational evidence is also supported by experimental work where small palm seedlings were exposed to repeated defoliation (McPherson & Williams, 1998; cf. also Anten *et al.*, 2003). Hence, a series of consecutive years with unfavourable climatic conditions will eventually kill smaller plants (cf. Walther, 2003). On the contrary, limiting frost damage in the winter season reduces the number of GDD₅ necessary to replace mass and resume growth (for further details see Fitzroya, 2004).

With this background, it is clear that although the cultivation of adult plants has been possible for decades in the past in the area at the southern foot of the Alps (and more recently in other areas north of the global palm distribution; cf. Fig. 1), regeneration south of the Alps has not been successful until the last few decades when there were consecutive years of climatic conditions above the critical threshold. This time lag in chronology between introduction and spread, the mechanistic understanding of the ecological impacts of sub-lethal freezing in winter, and the present restriction of sub-spontaneous palm populations to forest stands on southern exposed slopes of lower altitudes (cf. Berger & Walther, 2006) strongly suggest that an ameliorated climate, especially warmer and shorter winter seasons, was the essential prerequisite for palms and other evergreen broad-leaved species to become locally established (Walther, 2002b). The species' specific threshold parameters derived from habitat requirements in the native range (see Fig. 2) and applied to long-term climate measurements in the introduced range (Fig. 4) are in agreement with this climate change explanation (cf. also Beerling *et al.*, 1995). This explanation is further supported by the results of a bioclimatic model, which highlighted the range of potential suitable habitat in the introduced range at different periods in the past and present (Fig. 5). Periods with a continuous suitable climate have not occurred until the last few decades, allowing species to establish and naturalize locally. Additionally, these new wild populations of palms south of the Alps have reached a life stage and population size that makes them independent of seed supply from planted individuals in gardens and parks, and guarantees the long-term survival of a new northernmost palm population provided the ameliorated climatic conditions of the last few decades continue.

The rejuvenation of *T. fortunei* has not only been observed in southern Switzerland; the same species is reported to seed freely in gardens along the southern coast of Great Britain (e.g. C. Evans & J. Jones, pers. comm.), but there it is still restricted to garden areas and small individuals and, thus, to an early stage of a (potential) invasion process (G.-R. Walther, pers. obs.). In other more southern areas in Europe, more established *Trachycarpus* populations are reported (e.g. Kovacevic, 1998), whereas in parts of Australia (e.g. Groves, 1998) and New Zealand (e.g. Healy & Edgar, 1980; see also the New Zealand Plant Database <http://nzflora.landcare-research.co.nz>; Peterson *et al.*, 2006) *T. fortunei* is recorded as fully naturalized. In the USA, a reproducing *Trachycarpus* population is reported from the southern fringe of Austin (Texas) (L. Lockett, pers. comm.). In forest stands in Japan, increases in population sizes of *T. fortunei* have recently been reported from as far north as the Tokyo area (Kamei & Okutomi, 1992; Fujiwara & Box, 1999; Komuro & Koike, 2005).

Last, but not least, particularly in North America (Parker, 1994; Francko & Wilhoite, 2002; see also Gilman & Watson, 1994) and Europe (Stähler, 2000; Walther, 2002a, 2003), but also on other continents — though from the latter less information is publicly available — *Trachycarpus* has increasingly been cultivated even further beyond the potential range of palm distribution (see Fig. 1), which makes this particular species a 'cornerstone palm' in many parts of the world (Kembrey, 2004). The expected future global warming may thus not only facilitate the survival of the garden populations (Bisgrove & Hadley, 2002), but — in some areas — these garden populations may act as future dispersal centres for the further expansion of palms in response to continued amelioration of climate with global warming, thus allowing the spread and establishment of further palm populations similar to those of the southern foot of the Alps. Outputs from bioclimatic models, which are based on and validated with ground-truth data, may help to identify new areas where this process is likely to be detected in the near future, as shown on a European scale in Fig. 5.

Not only in Europe with *Trachycarpus*, but world-wide, palm species are benefiting from ameliorated climatic conditions. In parallel to the aforementioned situation at the southern foothills of the Alps, palms of other genera are extending elsewhere into new territories north of their former distribution. Increases in palm populations have been noted in south-western North America with the indigenous species *Washingtonia filifera* (Cornett, 1991), with *Sabal mexicana* in Texas (Lockett, 2004) and with *Sabal minor* in parts of Tennessee and other areas of the south-east USA where it is not native (D. Francko, pers. comm.) (see also Bjorholm *et al.*, 2005).

Hence, palms in general, and *T. fortunei* in particular, may serve not only as important indicators for the reconstruction of the past climate in the Earth's history (Mai, 1995; cf. also Brönnimann, 2002), but are also becoming significant global bioindicators across continents for present-day climate change and the projected global warming of the near future.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Realised and modelled distribution of *Trachycarpus fortunei* in its native range.

Appendix S2 Detailed chronology of establishment of the new northernmost palm population (synonyms: *Trachycarpus fortunei* (Hook.) Wendl. = *Trachycarpus excelsa* Wendl. = *Chamaerops excelsa* Thunb.).

Appendix S3 Pictures illustrating the different developmental stages of the new northernmost *Trachycarpus* population.

Appendix S4 Localities to the (non-exhaustive) compilation of *Trachycarpus* sites based upon literature and internet searches as well as personal observations and contacts (cf. Figs 1 & 5).

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