ORIGINAL PAPER

Quantitative genetic approach for assessing invasiveness: geographic and genetic variation in life-history traits

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Abstract Predicting the spread of invasive species is a challenge for modern ecology. Although many invasive species undergo genetic bottlenecks during introduction to new areas resulting in a loss of genetic diversity, successful invaders manage to flourish in novel environments either because of pre-adaptations or because important traits contain adaptive variation enabling rapid adaptation to changing conditions. To predict and understand invasion success, it is crucial to analyse these features. We assessed the potential of a well-known invader, the Colorado potato beetle (*Leptinotarsa decemlineata*), to expand north of its current range in Europe. A short growing season and harsh overwintering conditions are apparent limiting factors for this species' range. By rearing full-sib families from four geographically distinct populations (Russia, Estonia, Poland, Italy) at two fluctuating temperature regimes, we investigated (a) possible differences in survival, development time, and body size among populations and (b) the amount of adaptive variation within populations in these traits. All populations were able to complete their development in cooler conditions than in their current range. A significant genotype–environment interaction for development time and body size suggests the presence of adaptive genetic variation, indicating potential to adapt to cooler conditions. The northernmost population had the highest survival rates and fastest development times on both temperature regimes, suggesting pre-adaptation to cooler temperatures. Other populations had minor differences in development times. Interestingly, this species lacks the classical trade-off between body size and development time which could have contributed to its invasion potential. This study demonstrates the importance of considering both ecological and evolutionary aspects when assessing invasion risk.

Keywords Adaptation · Additive genetic variation · Geographical variation · Invasive species

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Introduction

The ability to predict the invasion of alien species is a general demand for modern evolutionary ecology because early detection is known to lead to the best eradication practice (Genovesi 2005). The invasion potential of diverse species has been estimated by using species' distribution models (e.g. Peterson 2003; Guisan and Thuiller 2005). These models are

based on a comparison between the ecological characteristics of the species' current or native range and those of the range the species could potentially occupy (e.g. Jeffree and Jeffree 1996; Roura-Pascual et al. 2004). Models typically assume that the species' ecological requirements in the original area will be conserved in the new area (Jeffree and Jeffree 1996; Roura-Pascual et al. 2004). This approach overlooks the fact that a species' fundamental niche may be much larger than its current realised niche (Fitzpatrick et al. 2006). Many invasive species show a niche shift in their introduced range (e.g. Parker et al. 2003), due to either selective environmental differences (e.g. the absence of natural enemies or availability of new resources) or rapid adaptation to the new conditions (Peterson 2003; Wiens and Graham 2005). Successful invasion, thus, does not necessarily require ecological similarity between the native and introduced range. Investigating species not as fixed entities but with a view to understanding the differences in their potential to change when arriving in new environments will further improve our predictions about both future invasions and species' long-term ecological success (reviewed in Sakai et al. 2001; Kolar and Lodge 2002; Parker et al. 2003; Gihlcrist and Lee 2007).

To understand the potential of species to expand their range, we need to assess both the ecological attributes (pre-adaptation) and the evolutionary potential (evolvability) of invasive species (Lee 2002; Gaston 2003). That is, we should know whether a species is able/unable to survive and reproduce in a new environment as well as whether the species can further adapt to the new conditions (Lee et al. 2007). The ability to survive beyond the current range can simply be studied by rearing individuals in conditions replicating those beyond the species' border (see, e.g. Griffith and Watson 2006; Lee et al. 2007). If all individuals are killed in the introduced range before they can reproduce, by, for instance, unfavourable temperatures, then the species cannot persist there. However, if some individuals survive, this may indicate that populations have genetic variability in relevant life-history traits which would enable them to change and adapt to new conditions, resulting in more viable individuals (Gihlcrist and Lee 2007). This can be studied via quantitative genetics by analysing the presence of additive genetic variance in important life-history traits (Hoffmann and Blows 1994; see also Lee et al. 2007). The absence of additive genetic variance in important life-history traits directly restricts species' range (Griffith and Watson 2006) and their potential to cope in the changing world (Hoffmann et al. 2003). Similarly, the presence of adaptive variability in important life-history traits can signify that a given species possesses the evolutionary capacity to respond rapidly to changing conditions which would, in turn, help it to further expand its range (Carroll and Dingle 1996; Garcia-Ramos and Rodriguez 2002; Lee 2002; Lee et al. 2007; but see Tsutsui et al. 2000).

An ideal species to study interpopulation differences in life-history traits in invasive species is the Colorado potato beetle, *Leptinotarsa decemlineata*, which has rapidly spread throughout the US and Europe (EPPO 2006). The beetle probably originated in Mexico from whence it spread to the US (Casagrande 1985). The beetle was accidentally introduced to France in the twentieth century and it spread rapidly almost throughout Europe (Johnson 1967). The most recent introduction has established populations in the European part of northern Russia where population densities are high. This increases the possibility that the species might expand its range even further. This species will allow us to assess the potential of an invader to further expand its range in the *introduced* area, an under-explored field of study in invasion literature. The species has a known invasion history, but its potential for future expansion is still unknown. The European populations of the beetle originated from a single invasion from the US containing only a fraction of the genetic variability present in North American populations (Grapputo et al. 2005). This founder effect could indicate that the European populations may have lost adaptive genetic variability in life-history traits and, consequently, be unable to evolve. The fact that the beetle has successfully colonised nearly all Europe suggests otherwise. In order to successfully establish beyond their northern border, beetles should be able to develop from egg to overwintering adult stage in a shorter time and in colder temperatures than in their current range and to overwinter successfully. This could be achieved by accelerating development without sacrificing size as a large body size is important for both overwintering success and a high reproductive effort (Roff 1992; Conover and Schultz 1995).

While fluctuating temperatures are the norm of natural environments, most laboratory experiments have been conducted at constant temperatures to minimize the environmental component of variance (Roff 1992). Brakefield and Kesbeke (1997) have led the current demand for conducting experiments with more natural conditions including fluctuating temperatures (see also Sgró and Hoffmann 2004) to obtain more generalized results applicable to natural populations and invasion biology. We reared full-sib families from four geographically discrete populations within the invasive range (Russia, Estonia, Poland and Italy) at two fluctuating temperature regimes. We assessed (a) whether there are differences in survival, development time, and body size among populations, which are expected to differ due to the seasonal- and daily temperature mean differences among these countries, and (b) the amount of adaptive variation within populations in the life-history traits relevant to invasion. Particularly our aim was to test whether and to what extent European populations possess genetic variation in important life-history variables which would fuel the invasion further north (Gihlcrist and Lee 2007). We used upper limit estimates of adaptive genetic variation so as to avoid under-estimation of species' invasion potential.

Materials and methods

Study insects

The beetles used in this experiment were descendants of field collected adults (collected in summer 2003) from Estonia (58°22′N), Poland (52°14′N) and Italy (41°13′N). A population was also collected from northern Russia (59°57′N [St. Petersburg]) and was maintained in a laboratory environment for three generations before the experiment to estimate the importance of maternal effects (see Kawecki and Ebert 2004). This laboratory population was collected from the field in Russia in autumn 2001 for overwintering and was reared to produce further generations in a greenhouse. At the collection sites in Russia the mean maximum daily temperature in June–August is 21.9°C (observation site: St. Petersburg), 22.3°C in Estonia (the nearest observation site: Pskov, Russia), 23.3°C in Poland (the nearest

observation site: Szczecin) and 27.5°C in Italy (observation site: Venice) (based on climatological data from Word Meteorological Organization).

We used a full-sib design because the beetles from Estonia, Poland and Italy had already mated in the field. The laboratory (Russian) population was generated by pairing beetles randomly. Our design gives broad-sense estimates of genetic variation as it includes common environment and dominance variance (Falconer and Mackay 1996; Roff 1997). However, invasion risk can be more securely predicted by using the upper limits of the additive genetic variation in the assessment. We collected eggs from 25 Russian, 22 Estonian, 40 Polish and 21 Italian females. The offspring of one female are hereafter referred to as a family. Egg masses were kept separate under a temperature regime of 18–25°C until hatching (see experimental set-up).

Experimental set-up

The experiment was carried out in two controlled environmental chambers (Type B1300, Weiss technic) housed at the University of Jyväskylä under a photoperiod of 4 h dark (night), 2 h dawn, 16 h light (day) and 2 h dusk. One chamber was set to a variable regime in which the temperature was 13°C during the night, warming up to 20°C during the dawn and 20°C throughout the day, declining back to 13°C during the dusk (average 17°C). The other chamber was set to a variable regime in which the temperature was 18°C during the night and 25°C during the day; warming up and cooling down during dawn and dusk respectively (average 23°C). The colder temperature regime corresponds to normal Scandinavian summer (June–July) conditions and the higher temperature regime reflects the conditions of an exceptionally warm summer (based on climatological data from the Finnish Meteorological Institute). The long-day photoperiod corresponds to the light conditions of the northern range of *L. decemlineata*. A high relative humidity was maintained by the use of open trays of water. As we had only two chambers, the analysis of the temperature differences is somewhat limited. However, all larvae were reared individually and thus the important population effects can be reliably estimated from our data.

We reared 218 Russian, 265 Estonian, 280 Polish and 328 Italian larvae. Hatched larvae were paired within a family by their weight (± 0.02 mg) (HA-180M/120M, A&D instruments) and then divided between temperature regimes (Family nested in population for ranked initial weight masses ANOVA $F_{1,976} = 1.996$, $P = 0.158$). Families within populations differed in hatching weight (nested ANOVA, $F_{102,976} = 8.891$, $P < 0.001$), whereas populations did not ($F_{3,110.931} = 1.475$, $P = 0.225$). These differences are unlikely to result solely from maternal effects because there was no correlation between offspring hatching weight (family mean) and dams' size (height of the left wing, which correlates strongly with adult weight [Pearson: $r = 0.739$, $n = 343$, $P < 0.001$]) in any population (Pearson $-0.486 < r < 0.05$, all $P > 0.129$), indicating that larger mothers did not produce larger offspring. These results imply that the maternal environment effects were not very strong and differences among families in hatching weight have a genetic basis.

Larvae were reared in Petri dishes lined with moist blotting paper and fed daily with fresh potato leaves (variety *Van Gogh*). Larval-to-adult survival (survive yes/no) and development times (in days) were recorded (first instar larva to adult). Adults were weighed (± 1 mg) (AM100, Mettler) on the day of emergence and sexed.

Statistical analysis

We performed a binary logistic regression on the survival data. In the model, a dependent variable was the probability to survive either as dead (0) or alive (1) at the end of the experiment, and independent variables were the population and temperature (as categorical factors), family and initial mass. Differences were tested with a Mann–Whitney tests (*p*-values adjusted with sequential Bonferroni procedure). Estimates of population differentiation, and of genetic variation within populations, for development time and adult size were obtained by means of a nested ANCOVA. Since hatching weight affects future survival in many insects (see, e.g. Mappes et al. 1996), hatching weight was taken as a covariate. Population and temperature were entered as fixed factors and family nested within population as a

random factor in the ANCOVA model. As the data on development time and adult size did not meet the assumptions of a parametric statistic, we ranked (rank assigned to ties by the mean) the dependent variables. Adult size was ranked by sex. Development time was ranked overall. The broad-sense heritability was calculated for development time and adult weight from the means squares of one way ANOVAs following formula in Roff (1997, page 41). Heritability estimates for development times were analysed from families which had more than two surviving offspring. Heritability estimates of adult size were estimated from families which produced more than two females or males that reached adult size. We calculated the additive genetic coefficient of variation as: $CV_A = 100 \times (\sqrt{h^2} \times V_P$ /trait mean), where V_P is the sample variance of the particular trait. Evolvability estimates were calculated by using the formula: $I_A = (CV_A/100)^2$ (Houle 1992). This gives an indication of the potential for selection to change the mean of a trait (Houle 1992). A value of $100 \times I_A$ can be interpret as a percentage trait change per generation as a response to selection (Hansen et al. 2003). Evolvability and heritability of development time were calculated for all populations separately. Since adult weight did not differ among populations, we combined the data of all populations and calculated evolvability and heritability of adult weight separately for both sexes at both temperatures.

Results

Survival

Larval-to-adult survival was unaffected by the interaction between temperature and population (Binary logistic regression, $\text{Wald}_3 = 2.731$, $P = 0.435$), indicating that temperature affected survival similarly in all populations (Fig. 1). Survival was lower at the colder temperature (Logistic regression, $\text{Wald}_1 = 11.808$, $P = 0.001$) (Fig. 1) and dependent on population ($\text{Wald}_3 = 9.086$, $P = 0.028$, Fig. 1). Survival rates differed among families (Logistic regression, $\text{Wald}_1 = 10.302$, $P = 0.001$), indicating genetic differences. Hatching weight affected larval survival (Logistic regression, $\text{Wald}_1 = 8.051$, $P = 0.005$): heavier larvae were more likely to survive.
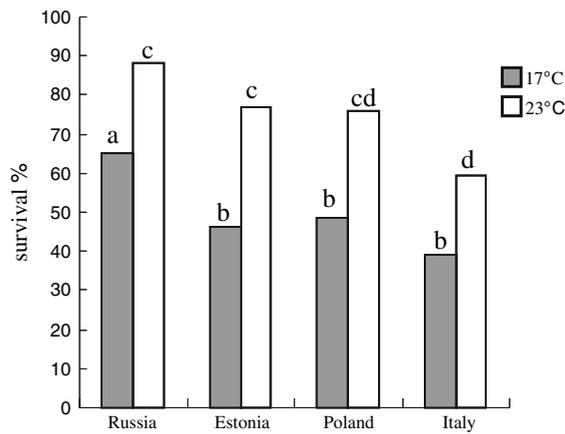
Fig. 1 Overall larval-to-adult survival for beetles from Russia (laboratory) ($n = 218$), Estonia ($n = 265$), Poland ($n = 280$) and Italy ($n = 328$) reared at two fluctuating temperature regimes. Black bars represent the lower temperature regime (mean 17°C) and white bars represent the higher temperature regime (mean 23°C). Bars marked with the same letter do not differ significantly in pairwise comparisons

Adult weight

Adult males were lighter than adult females (nested ANCOVA, $F_{1,87.887} = 156.56$, $P < 0.001$) and thus the sexes were analysed separately. A significant interaction between family and temperature in males indicated that families responded differently to different temperatures (Table 1). There was no interaction between family and temperature for females. Neither the main effect of population nor of family was significant for either sex. However, hatching weight affected adult weight significantly in males, but not in females. Russian males (LSD, $P < 0.001$) and females ($P < 0.001$), and Estonian ($P = 0.015$) and Italian females ($P < 0.001$) grew larger at the colder temperature. Estonian and Italian males and Polish males and females, in contrast, reached a similar body size at both temperatures (LSD, $P \geq 0.066$ for all tests). As the Russian population was grown in the laboratory longer and could have been more homogenous than other populations we tested whether our results were similar if it was not included in the analysis. The family by temperature interactions were similar as in the main analysis (nested ANCOVA, $F_{44,108} = 1.375$, $P = 0.094$ females; $F_{41,122} = 1.545$, $P = 0.036$ males).

Development time

Development time was not affected by sex (Table 2), therefore males and females were analysed together. The significant interaction between temperature and family (Fig. 2) indicated the presence of genetic variation for development time within populations. This interaction (nested ANCOVA, $F_{56,35.412} = 3.621$, $P < 0.001$) remained significant even if the Russian population was omitted from the analyses. Temperature strongly affected development times which were shorter at the warmer temperature (Table 2). The main effect of hatching weight and population also had an impact on development times.

Table 1 Nested analysis of covariance of adult weight in 108 families from four populations

Sex	Source of variation	df	Mean square	F	P-value
Females	Covariance (hatching weight)	1	4,371.05	0.74	0.393
	Temperature	1	209,606.03	28.38	0.001
	Population	3	5,821.09	0.87	0.461
	Family (population)	89	6,832.03	0.91	0.655
	Population × temperature	3	14,371.94	1.95	0.130
	Temperature × family (population)	57	7,565.17	1.27	0.127
Males	Covariance (hatching weight)	1	31,029.80	4.68	0.032
	Temperature	1	53,630.36	5.90	0.018
	Population	3	6,879.89	0.73	0.534
	Family (population)	85	9,995.58	1.08	0.383
	Population × temperature	3	10,366.02	1.14	0.339
	Temperature × family (population)	53	9,473.71	1.43	0.046

Table 2 Full model for nested analysis of covariance of development time in 108 families from four populations

Source of variation	df	Mean square	F	P-value
Covariance (hatching weight)	1	67,788.99	12.70	0.001
Temperature	1	8,599,280.52	661.06	0.001
Population	3	94,286.00	9.88	0.001
Family (population)	95	10,359.08	0.74	0.908
Sex	1	9,717.99	2.29	0.134
Population × temperature	3	3,335.86	0.26	0.855
Temperature × family (population)	74	13,622.99	3.57	0.001

Other interactions (sex × population; sex × temperature; sex × family (population); sex × population × temperature; sex × family (population) × temperature) were non-significant (for all tests $P \geq 0.233$) and are thus not reported

Under the colder temperature regime, Russian individuals developed significantly faster than individuals from the three other populations (LSD Estonian $P < 0.001$; Polish $P = 0.012$; Italian $P < 0.001$) and Polish individuals reached adulthood significantly faster than Italian individuals ($P = 0.011$). Other pairwise comparisons were non-significant ($P > 0.124$). Under the warmer temperature regime, individuals from Russia developed significantly faster than Italian, Polish or Estonian individuals (LSD Estonia $P < 0.001$; Poland $P = 0.003$; Italy $P = 0.001$) (Table 3). Other pairwise comparisons were not significant ($P \geq 0.391$ for all tests).

The relationship between development time and adult weight

Development time correlated negatively with adult weight (Fig. 3), indicating that fast-developing individuals became heavier than those that developed slowly. At the colder temperature, the correlation was significantly negative for both sexes of the Russian population (Pearson: males $r = -0.522$, $n = 45$, $P < 0.001$; females $r = -0.500$, $n = 34$, $P = 0.003$) and of the Estonian population (males $r = -0.429$, $n = 35$, $P = 0.010$; females $r = -0.417$, $n = 45$, $P = 0.004$), and for Polish males (males $r = -0.339$, $n = 45$, $P = 0.023$; females $r = -0.147$, $n = 44$, $P = 0.343$). At the warmer temperature, the correlation was significantly negative for both sexes of the Russian population (males $r = -0.504$, $n = 35$, $P = 0.002$; females $r = -0.499$, $n = 41$, $P = 0.001$) and for Estonian females (males $r = -0.306$, $n = 37$, $P = 0.065$; females $r = -0.405$,

$n = 31$, $P = 0.024$). The correlation between development time and adult weight was non-significant for Italian males and females at both temperatures (Pearson $P \geq 0.154$ for all tests) and for Polish individuals at the warmer temperature ($P \geq 0.117$ for all tests).

Heritability and evolvability

Heritabilities of development time at both temperatures differed significantly from zero, except for the Italian at the colder and Polish and Estonian populations at the higher temperature (Table 3). Heritabilities of adult weight were significantly different from zero for males at the lower temperature and for females at the higher temperature (Table 4). Evolvabilities of adult weight were of approximately the same magnitude for both sexes at the lower temperature, but not at the higher temperature.

Discussion

We assessed the invasion potential of *L. decemlineata* by estimating the ability to develop in cooler conditions than in their current range (pre-adaptation) and the amount of adaptive genetic variation in different life-history traits (evolvability) of four European beetle populations. Even the southernmost population was able to develop in the cooler conditions, which suggests that growing-season temperatures cannot solely explain the absence of *L. decemlineata* north of its current European range. We also found genetic variation for development

Fig. 2 Interaction between family and temperature for development times in Russian (laboratory), Estonian, Polish and Italian populations. Each line represents the reaction norm of one family
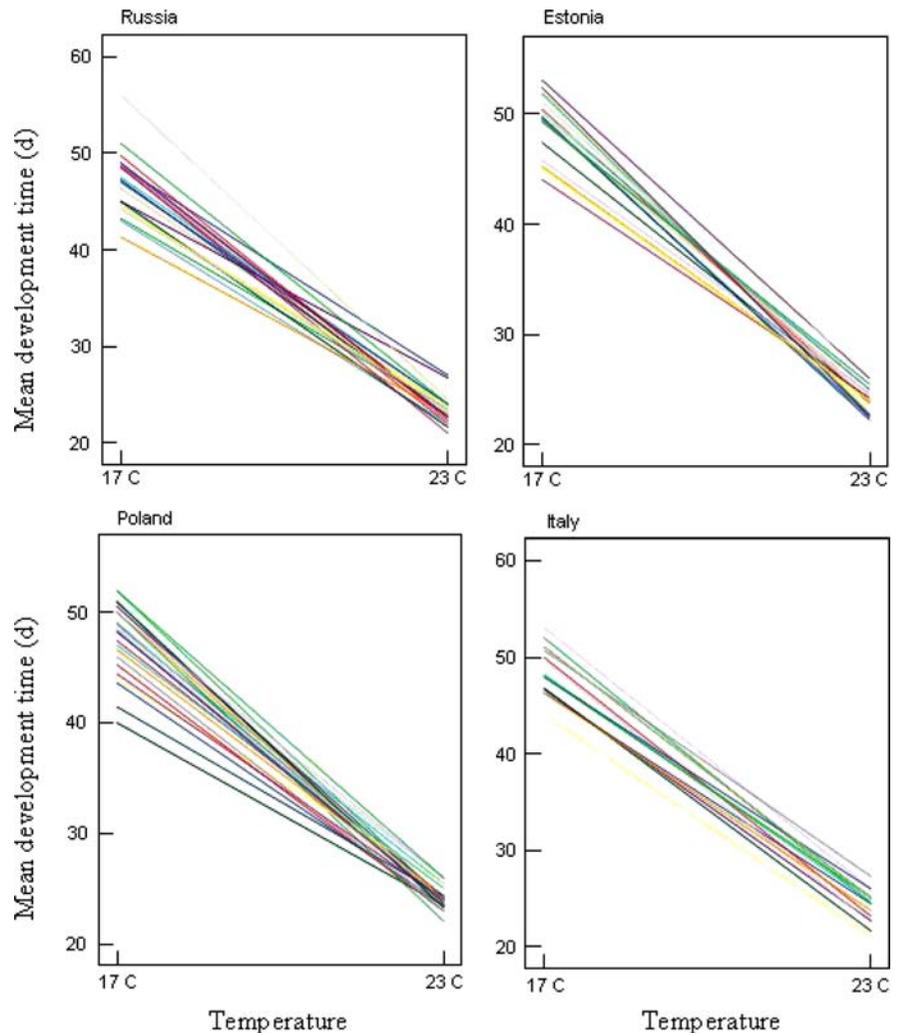
Table 3 Trait means (±SD), heritability h^2 ±SE (broad sense), coefficient of variation (CV$_A$) and evolvability % (IA) in development time for different populations

	n	Trait mean (day) (±SD)	h^2 (±SE)	CV$_A$	IA (evolvability %)
17°C					
Russia	77	46.40 (3.438)	0.635 (0.254)*	5.903	0.348
Estonia	79	48.94 (3.698)	0.567 (0.249)*	5.689	0.324
Poland	83	47.90 (3.402)	0.719 (0.253)*	6.022	0.363
Italy	77	48.52 (4.038)	0.277 (0.220)	4.383	0.192
23°C					
Russia	75	23.16 (1.917)	0.891 (0.246)*	7.816	0.611
Estonia	67	24.07 (2.032)	0.380 (0.267)	5.206	0.271
Poland	65	23.85 (1.406)	−0.094 (0.272)	N.E.	N.E.
Italy	63	23.97 (2.079)	0.920 (0.282)*	8.321	0.692

We included only those families in the analysis that had more than two individuals surviving to adulthood. Heritability coefficients shown by the symbol (*) are significantly different from zero. N.E. = cannot be estimated because of negative heritability coefficient

Fig. 3 Relationship between development time and adult size for (**a**) females at the higher temperature (23°C), (**b**) males at the higher temperature (23°C), (**c**) females at the lower temperature (17°C) and (**d**) males at the lower temperature (17°C). Populations are marked with *symbols*: Russia (laboratory) (●), Estonia (◇), Poland (□) and Italy (○). Each *line* represents the correlation between development time and adult size for one population
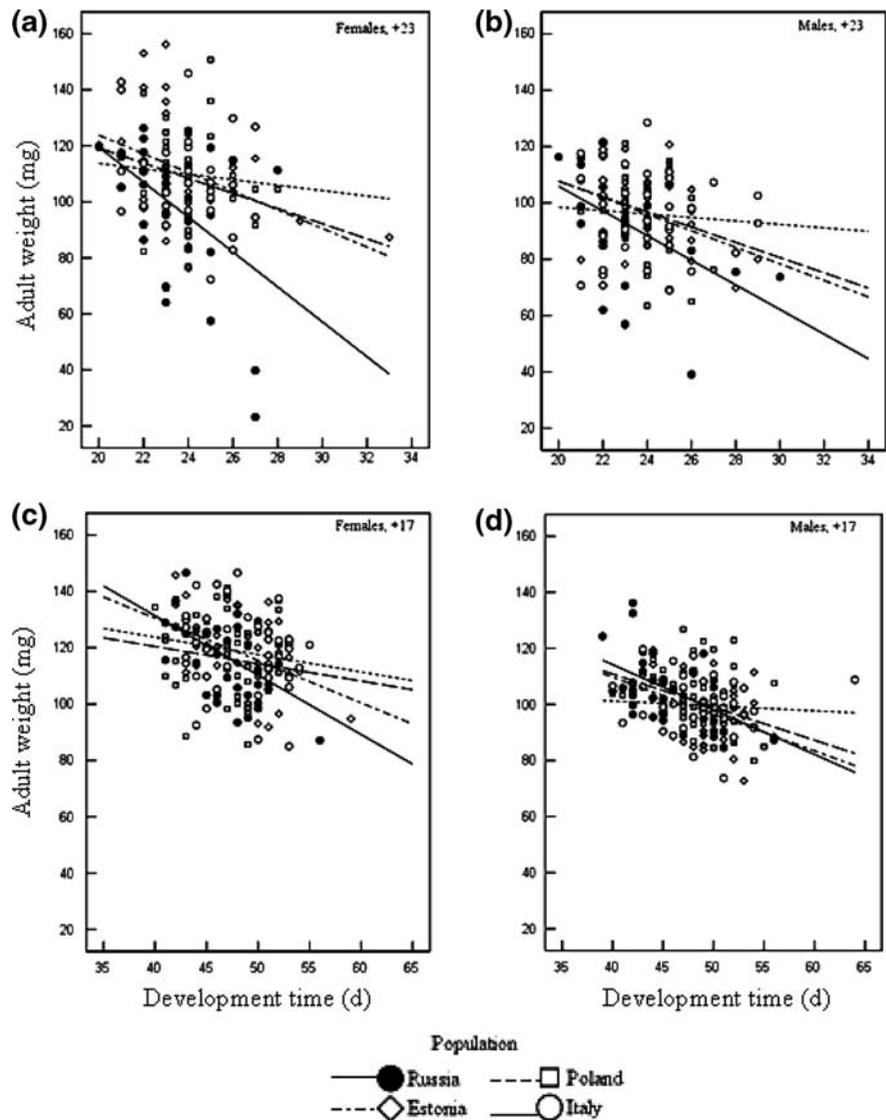
Table 4 Trait means (±SD), heritability h^2 ±SE (broad sense), coefficient of variation (CV_A) and evolvability % (IA) in adult weight for females and males under two fluctuating temperature regimes (populations combined)

	n	Trait mean (mg) (±SD)	h^2 (±SE)	CVA	IA (evolvability %)
17°C					
Females	135	116.52 (13.7)	0.227 (0.193)	5.601	0.313
Males	144	101.38 (11.1)	0.623 (0.187)*	8.653	0.748
23°C					
Females	103	106.48 (21.1)	0.547 (0.237)*	14.637	2.142
Males	123	95.53 (15.7)	0.066 (0.206)	4.227	0.179

Heritability coefficients shown by the symbol (*) are significantly different from zero

times, survival and adult male size within populations (Tables 1, 2). Differences in development times among families at the colder temperature were almost 2 weeks, which might be significant in a northern summer (Fig. 2). The genetic variation left in European beetle populations could therefore allow them to relatively rapidly respond to selection by a short growing season, leading to successful invasion *even* further north.

Temperature strongly affected all the life-history traits examined. A colder temperature not only increased development times (Table 3), but also decreased survival (Fig. 1). However, all populations were able to complete their life-cycle even at the colder temperature within the time-frame of the Scandinavian growing season. This suggests that this species has some pre-adaptations to tolerate conditions beyond its current northern border. This may be partly due to the photoperiod (L20:D4) used in this experiment which could have partly balanced the costs of cold temperature as individuals had more time to feed during the day. The short growing season in the north is also a challenge for successful overwintering. Beetles should reach a large body size before the onset of winter as heavier individuals not only have more lipid reserves (a fuel utilized during diapause), but they can dig deeper into the soil for overwintering and thereby gain more protection from frost during diapause (Noronha and Cloutier 1998). Life-history theory (Roff 1992) suggests that a trade-off would limit the simultaneous evolution of fast development and large adult size. This was not the case in the present study (see also Blanckenhorn 1994; Klingenberg and Spence 1997; Kause and Morin 2001; Forister et al. 2007). At both temperatures, fast-developing individuals became heavier than those that developed slowly, especially within the northern populations (Fig. 3). This atypical finding is not likely to arise from the lack of competition over food since the same result is found in various environmental conditions (Forister et al. 2007; Lyytinen et al. 2007). Rather the strong selection by pesticides (during early larval stages) as well as harvesting of potatoes twice (making food resource limited) in the season could have decoupled these traits. The fact that fast development time does not constrain size in this species gives an additional advantage for range expansion.

This species experienced a major bottleneck when introduced to Europe (Grapputo et al. 2005) evinced by the lower neutral genetic variability in European populations compared to American populations. While much information can be gained from measures of neutral genetic diversity, characterization of the genetic variation in life-history traits and the processes generating this variation are likely to be more important in determining potential invasion success (Lindholm et al. 2005). Interestingly, despite this reduction in neutral genetic variability (Grapputo et al. 2005), European beetles exhibited significant and relatively high heritability for development time (Table 3) and adult size (Table 4) (see also Loh and Bitner-Mathé 2005). Thus, these traits have the potential to respond to selection (see Roff 1997) and evolve in novel environments (Sakai et al. 2001; Lee 2002). This is important for invasion analysis, because it suggests that the beetle populations can adapt to cooler climatic conditions and, thus, could colonise a geographic area much wider than their current niche (EPPO 2006). A full-sib design may inflate the estimates (Falconer and Mackay 1996), which also include maternal effects, which means our heritability estimates show the upper limit of genetic variation. However, our estimates were near the same magnitude as evolvabilities calculated for other insect species (Blanckenhorn and Hosken 2003; Wagner et al. 1999). While direct comparisons among species and traits should be undertaken with caution (Houle 1992), using upper limit estimates of genetic variation reduces the risk of under-estimating the invasion potential.

One important source of variation among families and populations might be maternal effects. Maternal effects, whether genetic or environmental (food quality, temperature or photoperiod), can have a great influence on offspring life-history traits and fitness (Mousseau and Dingle 1991; Mousseau and Fox 1998; Fox et al. 1999; Holbrook and Schal 2004). Fox et al. (1999) showed that in seed beetles, *Stator prininus*, offspring from smaller females took ~0.5 days longer to develop than offspring from larger females. It is, however, unlikely that the variation in development times among families in our experiment could be the result of maternal environment alone as it was almost 2 weeks at the cooler temperature. Although families differed in hatching weight, there was no correlation between dam's size

and offspring's hatching size, indicating that larger dams do not produce larger larvae. Since families also differed in hatching weight within the laboratory population, we suggest that differences among families and populations could be explained by genetic differences rather than the maternal environment alone.

Differences among Estonian, Polish and Italian populations were minor, which might be explained by migration among them (see Grapputo et al. 2005). Substantial gene flow could have swamped adapted genotypes and thus prevented the evolution of local adaptation (Hoffmann and Blows 1994; Kawecki and Ebert 2004). The Russian population, instead, differed from the other populations by having a significantly shorter development time and a higher survival rate at both temperatures (Fig. 1, Table 3). One explanation is that these beetles were reared and overwintered in the laboratory for three generations while the other beetles were descendants of field collected adults. The laboratory population had possibly undergone a different selection than had the field collected individuals and had adapted to laboratory conditions. If such adaptation had occurred, it would suggest that the beetles could indeed respond quickly to different environmental conditions. However, parents of the Russian beetles were reared in warm conditions ($\sim 23°C$) which would not have favoured selection to colder temperatures. Alternatively, the detected differences reflected genuine local adaptation resulting from divergent selection. Selection by a colder climate in the Russian (northernmost) population may have produced and maintained a faster development time (see, e.g. Nylin et al. 1993; Conover and Schultz 1995).

We set out to assess the invasion potential of the Colorado potato beetle. The four beetle populations showed a wide temperature tolerance which would suggest that the beetle could flourish in habitats beyond its current range. Furthermore, our analysis of genetic variability revealed that European L. decemlineata still exhibit adaptive genetic variation in life-history traits, in particular for development times, indicating that there is potential for evolution in these traits. The beetle may even respond to selection by a colder climate. The ability to respond to selection by divergent natural selection manifested as population differentiation: the northernmost population reached the adulthood fastest and suffered the lowest mortality. We found no trade off between adult size and fast

development. In this respect, there is no selection acting against evolutionary change in these traits, improving the possibility of adaptation to high latitudes. Therefore, we suggest that the beetles could develop in the short time-frame necessary for colonising northern latitudes where summers are short without suffering small adult size. Our analysis shows that when predicting species' invasion, it is essential to consider evolutionary potential as well as pre-adaptation to an ecological niche (see Lee 2002; Sakai et al. 2001; Sax et al. 2005).

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