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Climate-mediated population dynamics enhance distribution range expansion in a rice pest insect

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Abstract

Environmental fluctuations can influence invertebrate population dynamics over large spatial scales, and effects of climate change are of particular importance in understanding phenology. In this study, we tested whether changing climate patterns could increase voltinism and emergence synchrony in *Stenotus rubrovittatus* and drive the mirid bug's expansion into currently uninhabited areas of Japan. This expansion could have potentially serious economic consequences for the rice industry. We modelled development of *S. rubrovittatus* in the field applying the effective accumulated temperature model to calculate the theoretical number of generations and the egg hatching dates from 2003 to 2012 based on a high-resolution, daily weather database. We then performed a regional analysis to assess the relationship between population dynamics and range expansion across the study region and also included a local analysis to evaluate how population parameters affect the presence of *S. rubrovittatus* at local sites in each year. Results showed that distribution expanded with a relative increase in voltinism and with synchrony of egg hatching date. Moreover, we showed that increased voltinism in the previous year positively influenced local population occurrence. This positive effect suggests that the species' distribution range expands through increased reproduction at both the regional and local scale. Climate-mediated population dynamics play a significant role in range expansion of the mirid bug.

Keywords: Climate change; Effective accumulated temperature; Mirid bug; Moran effect; Spatial synchrony

Introduction

Climate strongly influences insect population dynamics (Cammell & Knight 1992; Bale et al. 2002; Walther et al. 2002) through the modulation of survival rates, development rates, fecundity and dispersal (Kiritani 2006; Jepsen, Hagen, Ims, & Yoccoz 2008; Robinet & Roques 2010). These

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changes, in turn, can influence range expansion (Bale et al. 2002; Kiritani 2006; Le Roux & McGeoch 2008; Robinet & Roques 2010). Species distribution is easily observed, and consequently it is often used to measure the response of insect populations to a changing climate (Hickling, Roy, Hill, Fox, & Thomas 2006; Musolin & Fujisaki 2006; Musolin 2007).

Spatial synchrony of separate populations can arise from exogenous environmental factors, a phenomenon known as the Moran effect (Moran 1950; Koenig 2002; Liebhold, Koenig, & Bjornstad 2004; Allstadt, Liebhold, Johnson, Davis, & Haynes 2015). Spatial synchrony in the population dynamics of herbivorous insects can increase the severity of damage caused by an outbreak (Bjørnstad, Liebhold, & Johnson 2008; Liebhold, Haynes, & Bjørnstad 2012). Climatic conditions can force the Moran effect (Koenig 2002; Liebhold et al. 2004). For pest insects, a warming climate and changes in the frequency of climatic anomalies can affect both the intensity of population synchrony and range expansion, with potentially devastating impacts on plant health (Williams & Liebold 1995; Volney & Fleming 2000; Battisti, Stastny, Buffo, & Larsson 2006; Musolin 2007). Consequently, understanding the patterns and drivers of population dynamics could improve our ability to assess risks to species and develop effective insect management strategies (Bjørnstad et al. 2008; Allstadt et al. 2015).

Grain-feeding bugs cause major damage to rice (*Oryza sativa* L.) and other economically important grains worldwide (Nagasawa & Higuchi 2012). In Japan, the discoloration of rice grains caused by mirid bugs (Heteroptera: Miridae) is a serious economic problem for rice cultivation (Kiritani 2006; Yoshioka, Takada, & Washitani 2011; Takada, Yoshioka, Takagi, Iwabuchi, & Washitani 2012). For example, *Stenotus rubrovittatus* and *Trigonotylus caelestialium* are pests that damage or discolour rice kernels, and the formation of this pecky, or lower quality, rice has had serious economic consequences in Japan since the 1990s (Kiritani 2007; Yoshioka et al. 2011; Takada et al. 2012). Japanese rice quality regulations identify four grades of brown rice, based on the percentage of pecky rice (Ministry of Agriculture Forestry and Fisheries 2001). The higher the content of discoloured grains the lower the quality and grade and thus the lower the market price. Despite efforts to control these pests, their distribution continues to expand, and the resulting agricultural damage continues to increase (Watanabe & Higuchi 2006; Higuchi 2010; Ohtomo 2013; Tabuchi et al. 2015).

Kiritani (2006) suggested that climate warming increases voltinism in mirid bugs and their relatives. Thus, we hypothesised that mirid bugs expanded their current range in Japan as a result of synchronised increases in voltinism and/or outbreaks caused by recent changing weather patterns. Here we tested this hypothesis using *S. rubrovittatus* in the Tohoku region of northern Japan because (1) the distribution range of this species has increased over the last decade in this region (Tabuchi et al. 2015), (2) time-series distribution records are available and (3) the ecological characteristics of this species, particularly its response to climatic factors, are well studied (Higuchi 2010; Ohtomo 2013). We focused on the effects of temperature changes on voltinism and the synchrony of emergence timing in *S. rubrovittatus*. We predict (1) the number of annual generation increases with the expansion of the species' distribution range and (2) emergence timing tends to synchronise across populations, causing *S. rubrovittatus* outbreaks at both the local and larger spatial scales and resulting in range expansion. These predictions support our hypothesis that increased distribution of *S. rubrovittatus* has arisen not because the species is expanding into new regions that are now suitable owing to climate changes, but rather because of spillover from its current distribution range into new areas as a result of increasing population density. Actually, Kobayashi, Sakurai, Sakakibara, and Watanabe (2011) suggested that increased distribution of *S. rubrovittatus* was caused by a surge in local populations based on the polymorphisms of mtDNA.

We tested our hypothesis using the effective accumulated temperature (EAT) model for *S. rubrovittatus* as a parameter of the population dynamics. We calculated both the theoretical voltinisms and egg hatching dates at a 1-km resolution using daily temperatures recorded from 2003 to 2012 along with available distribution records of the species. If our hypothesis is supported, the distribution range of *S. rubrovittatus* would expand when the voltinism increases and/or emergence time is synchronised over a large spatial extent. Because the synchrony of increasing voltinism and emergence timing could occur at various spatial extents, we tested this hypothesis at both the regional scale and the local scale within the Tohoku region of Japan.

Materials and methods

Study region

The study was conducted in Akita and Yamagata prefectures, Japan, both of which lie in the Tohoku region and border the Sea of Japan (Fig. 1). Rice cultivation is a dominant agricultural sector in the region. In both prefectures, the mirid bug *T. caelestialium* was the dominant rice pest from the 1990s to the mid-2000s, with *S. rubrovittatus* becoming a major pest species beginning in 2005 (Watanabe & Higuchi 2006; Ohtomo 2013).

Study species

S. rubrovittatus feeds on the inflorescences of various Poaceae and Cyperaceae species and can produce more than three generations per year (Higuchi 2010). In northern Japan, overwintered *S. rubrovittatus* eggs hatch in June (Ohtomo 2013; Tabuchi et al. 2015). The overwintered eggs and first-generation adults inhabit pastures or semi-natural habitats dominated by Poaceae and Cyperaceae. When rice plants reach the heading stage, generally in early August (Ono,

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