Allee Effects: empirical analyses of wild British butterfly populations and theoretical implications for population synchrony

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Abstract

An Allee effect is a density-dependent process that can be responsible for the extinction of small populations. This thesis focuses on the detection of Allee effects, along with other density-dependent processes, and their influence on population synchrony. In chapter 2 I investigate the spatial variation in influential density-dependent processes and density-independent weather factors for the large skipper butterfly *Ochlodes sylvanus* across its British range. I find both qualitative and quantitative spatial variation in these processes and factors driving population dynamics. In chapter 3, I develop and test a Bayesian methodology, that I then use in chapter 4 to analyse local population level dynamics for 38 British butterfly species. For 35 of these species I found population level Allee effects and also found that phylogeny significant influenced a species' susceptibility to Allee effects. Finally, in chapter 5 I examine the influence Allee effects have on network population synchrony in a theoretical framework.

"What a very difficult thing it is to write correctly, I am only just beginning to feel my own inaccuracies"

(In a letter from Darwin to Henslow, 23rd Sept. 1837)

"Just like being in my own solar system
Doing good things but then totally eclipse them"

(Modest Mouse, Satellite Skin, 2009)

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Contents

Chapter 1: Introduction

1.1. A Review of Population Dynamics Literature

The focus of this literature review will be population ecology, with a greater emphasis on density-dependent processes. I first discuss generally why the study of population ecology is important and then move on to review literature relating to different forms of density dependence, namely negative density dependence and Allee effects. I review the evidence for both, using examples from studies that investigate populations in their natural environment and from experimental studies for which populations are analysed in artificial settings. I provide an account of methods used to detect density dependence and then present my first research chapter for which I investigated the spatial-variation in influential density-dependent processes and density-independent weather factors for the large skipper butterfly *Ochlodes sylvanus* across its British range. I find both qualitative and quantitative spatial variation in these processes and factors driving population dynamics. In chapter 3, I develop and test a Bayesian methodology, that I then use in chapter 4 to analyse local population level dynamics for 38 British butterfly species. For 35 of these species I found population level Allee effects and also found that phylogeny significant influenced a species' susceptibility to Allee effects. Finally, in chapter 5 I examine the influence Allee effects have on network population synchrony in a theoretical framework.

1.1.1. Importance of Population Ecology

Population ecology is concerned with how and why a population varies in size as a response to changes in the biotic and abiotic components of its surrounding environment.

It is vital to understand the impact of the ecological factors driving changes in population size so that predications can be made about a population's risk of extinction and about the requirements for population persistence. Making predictions about population extinctions is important as local extinctions have potentially devastating implications for species survival and ecosystem functioning. The preservation of species, either globally or locally, is essential because of the contribution each species makes to its ecosystem. The necessity of having multiple species per functional group, e.g. trophic groups such as autotrophs, within an ecosystem has been debated at great length in ecology (May 1972; Ehrlich & Ehrlich 1981; Walker 1992; Naeem 1998). However, experimental evidence has shown that different ecosystem processes respond differently to loss of biodiversity and increased number of species per trophic group leads to more reliable ecosystem functioning (Naeem *et al.,* 1994; Naeem & Li, 1997). More recently increased biodiversity has been linked to enhanced provisioning of ecosystem services, e.g. nutrient cycling (Chapin *et al.*, 2000; Dobson *et al.*, 2006). Elevated ecosystem functioning and ecosystem services provide a strong argument for the conservation of all kinds of species (Power *et al.*, 1996; Dobson *et al.*, 2006). The risk of population level extinction may be increased by demographic stochasticity due to random variations in births, deaths and sex-ratios, environmental fluctuations and catastrophic perturbations such as landslides destroying a whole montane habitat or a forest being completely logged (Pimm & Redfearn, 1988). Demographic and environmental stochasticity amplifies vulnerability to extinction when populations are small, declining or fluctuating with large intensities (Mace *et al.*, 2008).

Analysis of population dynamics has been used to address problems in resource management. For example, Myers *et al.* (1995) examined the population dynamics of commercially valuable fish species to investigate the effects of overfishing. Population

ecology is also central to challenges in pest control (Amman & Logan, 1998; Lockwood & Lockwood, 2008), species invasions (Ferguson *et al.*, 1994; Liebhold & Bascompte, 2003) and disease spread (Grenfell et al., 2001), where understanding population dynamics of species can be economically and medically important. Identifying the factors responsible for population fluctuations is not always an easy task though (May, 1986) and numerous influential factors often work simultaneously. Drivers of population dynamics include habitat fragmentation (Wiegand *et al*., 2005; Strohm & Tyson, 2012), habitat degradation (Griffen & Drake, 2008) and climate (Thomas *et al.*, 1994; Boggs & Inouye, 2012). Changes in population size not only occur in response to changes in the environment, they are also influenced by population density. Nicholson (1933) defined this as the "balance of nature". This will be the focus of the next section of this literature review.

1.1.2. Population Regulation Towards an Equilibrium

Thomas Robert Malthus' *An Essay on the Principle of Population*, first published in 1798, raised concern about the possible social and economic consequences of increased human population growth. He predicted that population increase would lead to much worse conditions for the poor:

> *"food therefore which before supported seven millions must now be divided among seven millions and a half or eight millions. The poor consequently must live much worse, and many of them be reduced to severe distress"*
>
> *(An Essay on the Principle of Population, Chapter 2, pp 19)*

Nicholson (1933) highlighted that competition between conspecifics for resources was also evident in nature, and that this leads to a population potentially being regulated around an equilibrium level of density. Population regulation around an equilibrium is known as density dependence and can be found in a number of qualitatively different forms. When a population is being regulated towards an equilibrium the population is experiencing negative density dependence. When a population grows, the resources per individual are reduced and survival and/or reproductive fitness decreases (Banks & Thompson, 1987; Drake & Ungar, 1989), causing the population to decline. Conversely, declines in population density result in an increase in resources per individual. In this case, survival and/or reproductive fitness increases causing the population to grow. In this example, population regulation is driven by resource limitation. If a regulated population deviates away from the equilibrium, population density will be driven back towards it. Intraspecific competition may also lead to cannibalism at high population density. Cannabilism reduces the number of potential competitors for resources, as well as providing nutrition. As the population density decreases, cannibalism also decreases until the population begins to increase again, and the population is therefore regulated around an equilibrium (Turchin, 1999). Cannibalism has been shown to regulate populations of giant damselfly *Megaloprepus coerulatus* (Fincke, 1994) and blue crab *Callinectes sapidus Rathbun* (Moksnes *et al.*, 1997).

Natural enemies may also cause population regulation. The presence of natural enemies causes the formation of predator-prey and parasidoid-host dynamical systems. Predators kill and consume their prey, whereas parasitoids live in or on their host organism. Parasitoids will usually cause the host to die after feeding on the host for a period of time (Hassell, 2000). As prey numbers increase, predator numbers increase due

to increased predator birth rate and/or decreased predator mortality rate which result from an enhanced availability of food. However, as the number of predators increases the death rate of the prey increases reducing the number of prey (Volterra 1931; McPeek & Peckarsky 1998). Predator-prey systems may possess a range of qualitatively different population dynamics, such as stable point equilibrium, and cyclic or non-cyclic fluctuations in population size (Murdoch & McCauley, 1985). Stable point equilibria and stable cyclic behaviours in both predator and prey populations are fixed by intrinsic demographic rates, such as birth rate, predation rate and population growth rate (May, 1976), and stochastic effects due to random demographic and environmental variation (Hassell, 2000). Tanner (1975) showed that stable prey population dynamics resulted when the prey population's intrinsic growth rate was lower than that of the predator population, due to predator-prey interactions. In instances when the prey population's intrinsic growth rate was higher than that of the predator, stability was due to intraspecific competition. Tanner (1975) also suggested that the cyclic dynamics of the snowshoe hare-lynx predator-prey system was likely due to their intrinsic growth rates being approximately equal. McCauley and Murdoch (1987) showed that the oscillations observed in freshwater zooplankton *Daphnia* and its algal prey were also caused by predator-prey interactions, and not by periodic environmental factors as previously thought. However, a recent study examined the impact of environmental change on predator-prey interactions and found that temperature caused changes in herbivore and plant abundances (O'Connor *et al.*, 2011). Studies like O'Connor *et al.* (2011) are essential for developing our knowledge of how species interactions will vary under different temperature regimes and are extremely important for predicting the consequences of climate change. O'Connor *et al.* (2011) used metabolic theory to create their herbivore-

plant models and provide an example of how incorporating metabolic elements, such as energy conversion efficiency, can be useful to understanding predator-prey interactions.

Host-parasitoid systems have a similar array of dynamical behaviours as predator-prey systems (Hassell, 2000). Host-parasitoid systems are of particular interest because of their role in biological pest control (Childs *et al.*, 2004). Pest species may be kept at stable low densities by the regulatory effect of parasitoids for which the pest is their host. An example of successful pest control via parasitoids is the control olive scale *Parlatoria oleae*, which was responsible for a costly reduction in olive production, by *Coccophagoides utilis* and *Aphytis paramaculicornis* in California (Murdoch *et al.*, 1984). Other examples of pest controlling parasitoids include *Encarsia formosa* used to control pest whitefly *Aleyrodidae* (Jiang *et al.*, 1999), *Gonatocerus ashmeadi* used to control glassy-winged sharpshooter *Homalodisca vitripennis* (Grandgirard *et al.*, 2009), and tachinid flies *Cyzenis albicans* and the ichneumonid wasp *Agrypon flaveolatum* used to control the winter moth *Operophtera brumata* (Roland & Embree, 1995).

Many natural predator-prey and parasitoid-host dynamics are complicated by their interactions with other species in their communities (Bonsall *et al.*, 2004; Allesina & Tang, 2012). For example, complex food webs with multiple species at each trophic level may cause a predator's population dynamics to be driven by the abundance of multiple prey, each with differing impact on predator numbers. In the example of biological control of the olive scale *A. paramaculicornis* alone was not able to control the scale, but when both *A. paramaculicornis* and *C. utilis* were released together biological control was much more effective. *A. paramaculicornis* are actively parasitic from fall until spring, at which point increased heat incapacitates this parasitoid and the presence of *C. utilis* becomes important for continued regulation of the olive scale (Huffaker *et al.*, 1986).

Population dynamics of prey/hosts and their natural enemies are further complicated by spatial influences that are driven by dispersal and the Moran effect, which occurs due to spatially correlated extrinsic factors, such as weather. The impact of spatial factors have been demonstrated for both predator-prey (Holland & Hastings, 2008; Vasseur & Fox, 2009) and host-parasitoid (Bonsall *et al.,* 2002; Strevens & Bonsall, 2010) systems.

Many theoretical studies have explored the consequences of population regulation towards an equilibrium density on population dynamics by modelling various density-dependent mathematical functions (Verhulst, 1838; Pearl & Reed, 1920; May, 1974; Bellows, 1981). Resultant population behaviours include stable points where a population remains at its equilibrium population density and stable cycles where the population oscillates between limit points. Chaotic oscillations may also be produced by density-dependent processes. Chaotic oscillations are bounded population dynamics, i.e. the population oscillates between an upper and lower density with oscillations that show no repeating pattern throughout time. These oscillations are not due to any external factors and result only from the combination of population growth rate, density dependence and initial population density (May, 1974). Theoretical studies such as these show the wide range of possible population dynamics, and are therefore important for understanding and explaining the dynamical patterns observed in wild populations.

The form of density dependence that has been discussed thus far is negative density dependence as per capita growth rate has a negative linear relationship with population density. Negative linear density dependence causes population decline as population density rises above the equilibrium density due to the fitness of each individual decreasing. Conversely, when population density falls below the equilibrium individual fitness increases and the population grows. Within the negative linear density

dependence framework, therefore, at low densities individual fitness is at its highest. However, there are many ways in which low population density can be detrimental to individual fitness, which consequently may lead to a positive relationship between per capita population growth rate and population density at low densities. This form of density dependence is known as an Allee effect and will be the focus of the next section of this literature review.

1.1.3. Allee effects

Walder Clyde Allee's seminal work on animal aggregations considered the role of cooperation as one of the key elements that drove the evolution of sociality (Allee, 1931). Later, Walder Allee and Howard Odum examined the impact beneficial aggregations have on population dynamics (Odum & Allee, 1954). They showed that at very low population densities the benefits of gregarious behaviours are weakened. This reduces individual survival and reproductive ability, causing the population to grow at a slower rate or, in fatal cases, decline to extinction, i.e. positive density dependence occurs at low densities. This form of positive density dependence is known as a demographic Allee effect.

A number of mechanisms driving a demographic Allee effect have been identified (Courchamp *et al.*, 2008) and are usually related to either fecundity or survival. Fecundity related demographic Allee effects arise when reproductive output declines with decreased population densities. This is the case when an individual's ability to find mates is reduced at low densities. For example, laboratory-reared virgin female gypsy moth *Lymantria dispar* were tethered to trees in areas known to be populated with wild gypsy moths, and baited traps were placed near to the tethered females (Sharov *et al.* 1995; Tcheslavskaia *et al.* 2002). After 24 hours, the number of females that had been

successfully located and mated by males was recorded, along with the number of males found in the traps. The probability of females being mated had a positive relationship with the number of males in their adjacent traps. While many species are well adapted to successfully finding receptive mates, small perturbations in mate finding strategies, such as pheromone markings and calls, may result in mate-finding Allee effects at low densities (Courchamp *et al.*, 2008).

Simply finding a potential male to mate with may not be sufficient for species in which receptive females adopt mate choice strategies to improve offspring survival and fitness, e.g. via paternal care or enhanced genetic fitness of the offspring (Jennions & Petrie, 1997; Moller & Thornhill, 1998). At low densities mate choice is reduced and can contribute to the presence of demographic Allee effects, as has been found for Atlantic cod (Rowe *et al.*, 2004). Diminished mate choice occurs in a number of exploited crustacean stocks where larger, more profitable males are removed for sale, forcing females to mate with less suitable males. Large spiny lobster (*Panulirus argus* and *Jasus edwardii*) males fertilise significantly larger clutch size than smaller males, and therefore the removal of large males causes reproduction to be sperm-limited when mate selection is reduced (MacDiarmid & Butler, 1999).

The ability to find suitable receptive mates may be mediated by increased movement within a habitat patch of individuals when at low density. This effect was found in the bush cricket *Metrioptera roeseli* in an experiment that showed evasion of a demographic Allee effect was possible through increased mobility (Kindvall *et al.*, 1998). Conversely, the enhanced movement of individuals away from their current habitat patch in search of higher quality patches elsewhere may exacerbate an Allee effect in the habitat patch from which individuals are emigrating from. The proportion of emigrating

males from populations of Glanville fritillary butterfly *Melitaea cinxia* increased with decreased population density and resulted in a lower proportion of mated females (Kuussaari *et al.*, 1996). These conflicting consequences of elevated movement on Allee effects may be due to spatial structure (and its facilitation to emigration) or interspecies differences, such as mobility.

Reduced fecundity at low population densities may also be caused by reduced reproductive facilitation (Courchamp *et al.*, 2008). Breeding success in captive pairs of black lemurs *Eulemur macaco* and mongoose lemurs *Eulemur mongoz* is higher when females are kept in enclosures next to additional conspecifics compared to when they were completely isolated from other conspecifics (Hearn *et al.*, 1996). In this case mate finding ability is not a limiting factor and so reproductive facilitation is thought to be responsible for reduced reproduction at low densities. Per capita reproductive success is elevated with flamingo flock size due to higher exposure of reproductive displays by other flock members (Stevens & Pickett, 1994).

The timing of reproduction can be a key factor in determining reproductive success. Individuals within a population may be reproductively active at different periods of time within a breeding season (Calabrese & Fagan, 2004). This is known as reproductive asynchrony and has evolved in certain species to counteract detrimental impacts of seasonal variation in conditions that affect survival of young, e.g. temperature, food availability or predation (Brinkhof, 1993; Sih & Moore, 1993; Olsson & Shine, 1997; Calabrese *et al.*, 2008). While reproductive asynchrony may be beneficial to young survival when population density is relatively high, it may cause a reduction in average mating probability and lead to reduced mating success across a population. This is a consequence of a lowered number of overlapping male-female periods of active

reproduction and a lowered number of days when overlaps occur (Calabrese & Fagan, 2004).

Aggregations occur within populations to increase individual survival and avoid population-level demographic Allee effects. Overall survival is increased when the benefits of aggregating outweigh decreases in individual fitness due to, for example, increased competition or increased disease spread. Benefits from aggregating include thermoregulation, reduced predation per capita and enhanced feeding efficiency. Thermoregulation is achieved by aggregating groups of overwintering Alpine marmot populations that would otherwise not survive the cold (Stephens *et al.*, 2002), and is one of the benefits to overwintering aggregations of monarch butterflies (Wells *et al.*, 1998). Per capita predation can be lowered, depending on the nature of predation, by gregarious behaviour due to a decrease in the probability of predation per prey as population density increases. Reduced per capita survival rates with decreased population density due to predation have been shown to occur in *Daphnia-Chaoborus* (Kramer & Drake, 2010) and bighorn sheep-cougar *Ovis canadensis-Puma concolor* (Bourbeau-Lemieux *et al.*, 2011) predator-prey systems. Aggregation may also promote more effective feeding in, for example, sweet potato weevil *Cylas formicarius* (Sakuratani *et al.*, 2001) and African wild dog *Lycaon pictus* (Courchamp & Macdonald, 2001). *Cylas formicarius* use the tuberous roots of sweet potatoes for habitat and food. When feeding they produce secretions that make the tuberous root more favourable for egg and larvae survival. At low population density overall secretion is low and mortality of eggs and larvae is high (Sakuratani *et al.*, 2001). *Lycaon pictus* enhances feeding by hunting in packs. Simultaneous attacks cause lower energy cost per individual, while coordinated halting and pulling apart of prey allows more efficient killing and eating. Group intimidation also

reduces the risk of the kill being lost to kleptoparasites (Courchamp & Macdonald, 2001). There are a number of other benefits associated with packs including enhanced protection for young against predators. Packs carry out more sophisticated forms of cooperation compared to simple aggregations of individuals. Packs usually consist of one or few breeding pairs and many 'helper' subordinate individuals, resulting in different individuals having different roles within the group. A whole suite of cooperative behaviours result from pack dynamics and therefore the consequences of low population density on pack size and pack dynamics is of great conservation concern (Courchamp & Macdonald 2001).

Mechanisms that cause a reduction in individual fitness at low population densities are, in contrast to demographic Allee effects, called component Allee effects and may be counteracted by benefits associated with reduced population density, e.g. enhanced resource availability per capita. If the detrimental consequences of a component Allee effect are counteracted in this way, a demographic Allee effect (reduction in per capita growth rate with reduced population density) will not occur. If a population grows at a slower rate as density declines, the demographic Allee effect is weak, and if a population begins to decline as density is reduced the demographic Allee effect is strong. Kramer *et al.* (2009) highlighted the difficulty in distinguishing between weak and strong Allee effects and the importance of developing ways in which the strength of Allee effect can be estimated so that better assessments of a population's risk of extinction can be made. Lande (1998) demonstrated that random variation in births and deaths (demographic stochasticity) could amplify the extinction risk created by an Allee effect, highlighting the need to consider both demographic stochasticity and Allee effects when carrying out conservational evaluations of a population or species.

1.1.4. Detection of Density Dependence

Although many theoretical studies had examined population regulation by the early 1990s, few empirical investigations had provided support for the existence of density dependence in natural populations (Turchin & Taylor, 1992). Godfray & Hassell (1992) attributed this lack of detection of density dependence to the statistical problems associated with testing short runs of population data. Woiwod and Hanski (1992) addressed this problem by investigating the density dependence of 5715 time series of abundances of moth and aphid species. They found that detection of density dependence was indeed elevated with increased time series length from 10 to 24 years, and that 79% of moth and 88% of aphid time series consisting of more than 20 years showed evidence of density dependence.

The methods used by Woiwod and Hanski (1992) did not take into account the measurement error inherent in the moth and aphid census data they were analysing. Measurement error in census data may include observation error and sampling error (Clark & Bjornstad, 2004; Freckleton *et al.*, 2006; Hosack *et al.*, 2012). Observation error occurs due to variation in monitoring accuracy between observers and incorrect identification of species. Sampling error occurs when only a small portion of a larger population is being sampled and is generally true for all population data collected. Sampling error arises because the small portion being sampled (often referred to as a subpopulation) may not reflect the wider population's overall behaviour. Dennis and Taper (1994) developed likelihood ratio methods to account for measurement error. More recently, Bayesian approaches have been utilised to account for measurement error (Hosack *et al.*, 2012; Bonsall, Dooley *et al.*, 2013). Bayesian approaches are also advantageous over other statistical methods in a number of additional ways, such as

accounting for missing data and data from different sources. In this review, however, I focus on the key features of Bayesian methods that are important for detection of density dependence in population data. These are measurement error and process error, both of which are closely tied to model complexity. Process error may include demographic stochasticity which is the variation arising from random differences among individuals within a season and environmental stochasticity which is the variation due to unexpected or unpredictable environmental events that may influence population change.

Frequentist statistics allow conclusions to be drawn based on the frequency of the data supporting a testable hypothesis. Because of this, frequentist statistics require relatively large datasets and model simplification in order to increase statistical power and provide strong evidence for the results. By contrast, Bayesian approaches allow high levels of complexity to be incorporated into models by utilising a hierarchical framework (Clark, 2005). In frequentist approaches high complexity can often lead to overfitting. If a large enough number of explanatory variables are tested there is an increased chance that a subset of these variables will fit the given data, but if additional data are added to this set, e.g. more annual abundances, the new subset of variables now fitting the data may be quite different. The predictability of overfitted explanatory variables is therefore low. In hierarchical Bayesian frameworks, elevated complexity can be included without the risk of overparameterisation and overfitting. Complex hierarchical models provide the opportunity to partition out different types of error and allow each to be estimated separately (Clark, 2005). Hierarchical Bayesian frameworks are therefore very useful in testing for density dependence in population data (Clark & Bjornstad, 2004). Bayesian methods have been utilised to investigate density dependence in the mallard duck *Anas platyrhynchos* and canvasback duck *Aythya valisineria* (Viljugrein, 2005), bighorn sheep

Ovis canadensis (Colchero *et al.*, 2009) and three bird species *Gymnogyps californianus, Amazona vittata* and *Accipiter nisus* (Hosack *et al.*, 2012), with each study accounting for the unique form of measurement error associated with the data collected for each species.

Chapter 2: Spatial-variation in the magnitude and functional form of density-dependent processes on the large skipper butterfly *Ochlodes sylvanus*[1]

2.1. Introduction

The focus of this first research chapter is spatial ecology. Understanding the underlying ecological processes that govern population dynamics is essential for assessing the risk of extinction faced by a population. Furthermore, understanding how these ecological processes differ across space aids the evaluation of extinction risks faced by a species. Population dynamics are governed by a variety of ecological processes that are driven by a number of different density-dependent and density-independent factors (Sinclair & Pech, 1996; Rothery *et al.*, 1997; Benton *et al.*, 2006; Nowicki *et al.*, 2009).

A population may be regulated, through density-dependent processes, around an equilibrium (Turchin, 1999) and exhibit a negative relationship between population growth and population density (Nicholson, 1954; Rothery *et al.*, 1997; Strevens & Bonsall, 2010). Mechanisms by which this regulation is achieved may arise through the action of natural enemies (Hassell, 1985; Childs *et al.*, 2004; Liu *et al.*, 2007) and/or inter- and/or intra-specific competition which leads to limited resource availability (Royama, 1992). In contrast to this negative density dependence, a positive relationship between population growth and population density has been observed in the dynamics of many low density populations (Kramer *et al.*, 2009). Mechanisms related to fecundity and survival may be

[1] This chapter is a modified version of DOOLEY, C. A., BONSALL, M. B., BRERETON, T. & OLIVER, T. 2013. Spatial variation in the magnitude and functional form of density-dependent processes on the large skipper butterfly *Ochlodes sylvanus*. *Ecological Entomology*, in press. DOI: 10.1111/een.12055

responsible for this positive relationship. Those mechanisms associated with reproduction include mate finding ability (Kuussaari *et al.*, 1998; Tcheslavskaia *et al.*, 2002; Liebhold & Bascompte, 2003), reproductive facilitation, sperm limitation (Gascoigne *et al.*, 2009) and cooperative breeding (Courchamp *et al.*, 2008). Those mechanisms associated with survival include aggregation/thermoregulation, vulnerability to predators (Turchin & Kareiva, 1989), cooperative anti-predator behaviours and foraging behaviours (Courchamp *et al.*, 2008).

These mechanisms cause an Allee effect, the ecological process responsible for driving a local population to extinction below a threshold population density (Drake & Griffen, 2010). Above this threshold density the population dynamics may be driven by negative density dependent processes. If different density-dependent processes control a population within different ranges of densities, the observed relationship between population growth and population density is expected to be non-linear. Although numerous theoretical studies have been carried out on Allee effects, evidence of their existence in wild populations is limited (Kramer *et al.*, 2009; Gregory *et al.*, 2010).

Density-independent processes result from a number of density-independent factors such as weather (Pollard, 1988; Hoffman *et al.*, 2010) and habitat management, e.g. mowing (Johst *et al.*, 2006) and fire regimes (Hoffmann, 1999). Identifying the density-independent factors influencing a population's dynamics is key to understanding the changes observed in natural populations (Thomas *et al.*, 2011) and can be accomplished at a specified spatial scale (Pollard, 1988; Roy *et al.*, 2001). The type of influential density-independent factors and the type of density-dependent processes are often assumed to be consistent across the range of a species or throughout the selected study area (Rothery *et al.*, 1997; Roy *et al.,* 2001). However, some studies have shown

that population behaviours may differ across space (Hoffman *et al.*, 2010; Pasinelli *et al.*, 2011) suggesting that ecologically important factors and processes may vary both qualitatively and quantitatively across space. As density dependence is a possible driver of extinctions, through Allee effects, it is essential to evaluate the magnitude and functional form of density-dependent processes that govern population dynamics. This can be achieved by assessing the qualitative and quantitative variation in density-dependent (relative to density-independent) processes across space.

In this study I investigated population dynamics of the large skipper butterfly *Ochlodes sylvanus* (Esper) across its British range. *Ochlodes sylvanus* is a widespread species found throughout Europe and Asia, and has a distinct range edge in southern Scotland. Butterfly populations in their northern-most latitudes are at the limit of suitable climate (Dennis, 1993) and may experience habitat utilization restrictions (Thomas *et al.,* 2001). This may be due to peripheral populations being confined to relatively small areas where suitable microclimates are present (Oliver *et al.*, 2009). As habitat specificity of *O. sylvanus* is influenced by position within its British climatic range (Oliver *et al.*, 2009) and wide amplitudes in population size occur across its British range (Thomas *et al.*, 1994) I hypothesized that density-dependent processes and density-independent drivers of population dynamics will vary qualitatively and quantitatively across its British range.

Butterflies are ectothermic species and are highly sensitive to rainfall (Dennis, 1993). The impact of specific weather variables, to my knowledge, has not been investigated for the large skipper at a spatial scale smaller than the national level. Here, I considered a set of potentially important weather variables that correspond to time periods of the previous and current non-overlapping generations, as per capita growth rate from one generation to the next will depend on the fecundity of the previous

generation and larval and pupal survival of the current generation. In addition to density-independent weather factors I tested two forms of density-dependent processes: population regulation around a stable equilibrium and an Allee effect.

2.2. Methods

2.2.1. Study Species and Data

Ochlodes sylvanus is a univoltine, widespread species. Its UK distribution extends throughout Wales, England and southern Scotland, with no resident populations being recorded for Northern Ireland. For this reason I focused on regions in Britain alone. This species overwinters as a caterpillar and begins to pupate from early May. Adults emerge in late May and are on the wing until late August. I obtained indices of annual *O. sylvanus* abundance from the UK Butterfly Monitoring Scheme (UKBMS) database for each monitored site. These annual indices are derived by the UKBMS team from collated weekly transect data, and are used as a surrogate for local abundances (Rothery & Roy, 2001). The transect data consist of weekly fixed-route butterfly counts collected by recorders using a methodology outlined by Pollard & Yates (1993). It has been highlighted that caution is necessary when comparisons are made between species using the UKBMS data because of the difference in apparency between species (Dennis *et al.,* 2006). However, for any given individual species, variation in detectability between sites is small compared with the variation in true abundance**,** especially for the large skipper which is a highly detectable species (Isaac et al., 2011). Therefore, UKBMS data are well suited to this analysis.

The weather data available ran from 1971 to 2006 and therefore only butterfly indices within this time period were used. I calculated an index of annual population

density by dividing each annual abundance index by the corresponding transect area. I obtained weather data from the UK Climate Projections 2009 (UKCP09) database, which consisted of monthly mean temperature and rainfall for 5 km square grid squares of the UK Ordnance Survey National Grid collated by the Meteorological Office. To investigate the possibility of different density-independent weather factors being important to butterflies in different regions I tested 12 weather variables that corresponded to the distinct stages of the life cycle of *O. sylvanus* described above. These 12 variables consisted of site-specific measurements of mean temperature and mean rainfall for the previous year's spring (March, April, May), previous year's summer (June, July, August), previous year's autumn (September, October, November), current year's winter (previous year's December, January, February), current year's spring, and current year's summer. It was important to test a large number of weather variables so that the overall magnitude of weather effects could be accurately evaluated. Reducing the number of variables may have led to significant factors being overlooked, potentially underestimating the importance of weather on *O. sylvanus* population dynamics.

2.2.2. Statistical Analysis

Analysis was carried out for each 100 km square region (defined by the UK Ordnance Survey National Grid) occupied by *O. sylvanus* within its British range. Abundance indices from the time series for each monitored site within a 100 km square region were considered in the analysis of the dynamics of large skipper for that region. A 100 km square scale was used because a smaller scale would have resulted in insufficient data per region to test my hypotheses on the effects of multiple density-independent factors. Time series variance has been shown to vary with time series length (Pimm & Redfearn, 1988;

Inchausti & Halley, 2001). I confirmed this relationship to be present in the *O. sylvanus* data using an ANOVA test. The coefficient of variation (CV) for a time series varied with time series length (AOV: $F = 4.590$, d.f.= 31, 624, $p<0.001$). Fig. 2.1. shows three example time series of relatively low (a), medium (b) and high (c) CV. To account for this variation in time series between monitored sites I incorporated site as a random effect in my statistical analysis. In order to estimate density-dependent processes accurately, data corresponding to a previous year population density of zero were excluded. Zero densities produce per capita growth rates greater than or equal to one (log per capita growth rate ≥ 0), as a population of zero individuals can only increase in size, due to recolonisation, or remain at zero. These zero densities would mask the behaviour of population dynamics at low densities and were therefore eliminated from the analysis.

In order to investigate spatial variation I carried out an analysis that allowed the regions to be categorised in terms of their form of density dependence and influential weather effects. To identify and categorise a region experiencing an Allee effect I tested for positive linear and negative quadratic relationships between per capita growth rate and density. Allee effects only operate at low densities and therefore positive density dependence due to an Allee effect, would not be observed at high densities. If the observed densities for a given region are all low a positive linear relationship between per capita growth rate and density would be detected. However, above a certain density other density related processes may drive population dynamics. A negative quadratic relationship between per capita growth rate and population density over all densities would be indicative of a population exhibiting both an Allee effect at low densities and a density related regulatory process at high densities. I therefore tested for both quadratic and linear density dependence.

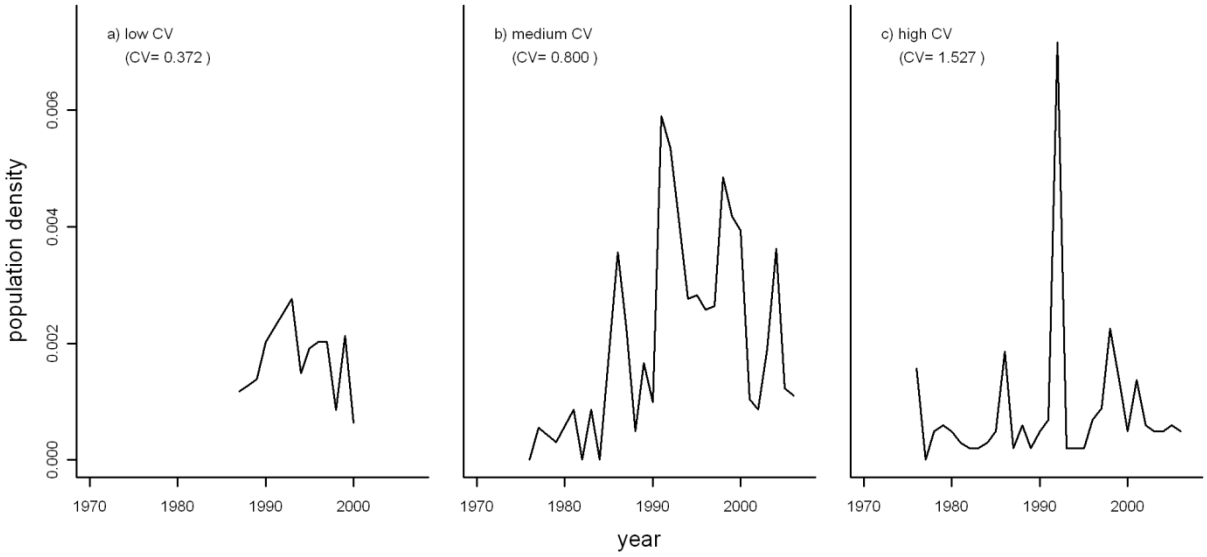

Fig. 2.1. Time series of individual *Ochlodes sylvanus* populations and corresponding coefficient of variance. Time series show examples of a) low, b) medium and c) high coefficient of variance. Sites are located in a) Dorset; OS grid reference SY809915, b) Cambridgeshire; OS grid reference TL650690, c) Cambridgeshire; OS grid reference TL210810.

Extremes in weather have negative effects on certain butterfly species (McLaughlin *et al.*, 2002; Roland & Matter, 2013), with the resultant relationship between per capita growth rate and weather having a negative quadratic shape. In this study I consider 12 weather factors and so testing for all quadratic weather effects would have involved the inclusion of 24 explanatory weather terms in addition to density terms. Statistical tests with such a large number of explanatory terms would require regions to have large data sets and would reduce the analysable area of the large skipper's range. I therefore wanted to include quadratic weather effects only if they were potentially important to large skipper population dynamics at the spatial scale of this study. I therefore produced a series of weather plots for each region after accounting for significant density dependence (Appendix A, Fig. A.1.). Visual inspection of these plots suggests that quadratic weather effects do not play a role in driving population dynamics in any of the 21 regions (Appendix A, Fig. A.1.). I therefore confined the analysis to only linear weather effects. This reduced number of weather variables allowed me to analyse each 100 km square region separately using the following mixed-effects model:

$$X_t - X_{t-1} = \underbrace{\alpha + \beta_1 X_{t-1}{}^2 + \beta_2 X_{t-1} + \gamma_1 W_1 + \cdots + \gamma_{12} W_{12}}_{\text{Fixed}-\text{effects}} + \underbrace{\mu_i}_{\text{Random}-\text{effects}} + \underbrace{\varepsilon}_{\text{Error}}$$

where X_t is the natural logarithm of population density in year t, and the W terms represent different weather variables (i.e. 12 W variables in total). α is the fixed-effects intercept. β and γ are fixed-effects slope parameters for density-dependent and weather variables respectively (i.e. 14 parameters in total). μ_i is the random intercept for each site, with normally distributed variance and zero mean. ε indicates residual errors which were

normally distributed with zero mean. Multiple stepwise regressions were carried out in R version 2.11.1 using the "*nlme*" package in order to obtain a minimum adequate model (MAM) for each 100 km square region (R Development Core Team, 2010; Pinheiro et al., 2011). Log of population densities were normally distributed for each region (Appendix A, Fig. A.2.) and therefore the lme (linear mixed effects) R function, which is suitable for normally distributed response variable, was used to run the regressions.

To assess the magnitude with which density dependence and weather influence population dynamics I evaluated two further models for each region. For the first model I dropped all density terms from the MAM, and for the second I dropped all weather terms from the MAM. I then estimated the percentage increase in Maximum Likelihood (ML) when the relevant variables were taken out of the statistical model. I used ML because I was comparing models with different numbers of parameters (Burnham & Anderson, 2002). A large percentage increase in the ML upon elimination of a set of variables reflected a large impact of those variables on population dynamics.

To identify potential evidence for weak and strong Allee effects I examined the number of equilibria exhibited for the regions with negative quadratic density dependence. Two equilibria can be associated with a strong Allee effect and one equilibrium can be associated with a weak Allee effect, and so regions with negative quadratic density dependence were easily categorised as having weak or strong Allee effects.

The parametric statistical method used also allowed the possibility of positive quadratic density dependence, a result suggesting that increased density is associated with increased per capita growth rate at the highest observed densities. The detection of this unexpected relationship at high densities could be attributed to the nature of this

analysis. While the parametric statistical method I have used allowed me to easily categorise regions by their form of density dependence it also meant that I needed to be cautious in the interpretation of quadratic relationships. A positive quadratic relationship with only slight curvature and a minimum at high densities could be indicative of a negative relationship between per capita growth rate and density with the strength of this relationship varying across the density range. To evaluate the possibility of this varying strength of density dependence across densities I carried out a piecewise regression to identify linear density dependence below and above the equilibrium density for regions showing positive quadratic relationships. First, I extracted residuals from a region's MAM including weather variables only in order to obtain log per capita growth rates adjusted to account for significant weather effects. Next, I fitted a mixed-effects model with quadratic density dependence over all densities and a mixed-effects model with two different linear density-dependent processes (one for densities smaller than that at the equilibrium and one for densities greater than that at the equilibrium) to each region's set of extracted residuals. To evaluate which of the two models best defines the relationship between population growth and population density I compared the models' Akaike weights (Burnham & Anderson, 2002) and mean squared errors (MSE). For one of the regions (OS grid reference SH), the ratio of regional sample size to numbers of model parameters was less than 40, therefore an adjusted AIC value (AIC_c) was used to calculate Akaike weights (Burnham & Anderson, 2002).

2.3. Results

A total of 21 of 100 km square regions were analysed. The mean number of time series within a region was 31 (SE = ± 7; range = 3 to 134) and the mean number of population growth estimates used for each region was 247 (SE = ± 67; range = 19 to 1283).

In one of the twenty one 100 km square regions log per capita growth rate was not significantly affected by any of the variables tested. The log per capita growth rate of the remaining 20 regions was significantly influenced by density dependence alone (3 regions), or a combination of both density dependence and density-independent weather factors (17 regions). No regions were significantly affected by weather factors alone. (See Appendix A, Table A.1. for a summary of variables in the minimum adequate model for each region). Three types of density dependence were observed; negative linear (14/20 regions), positive quadratic (3/20 regions) and negative quadratic (3/20 regions). Positive linear density dependence was not observed in any of the regions. In all 3 regions where the population exhibited positive quadratic density dependence just one equilibrium was found over the observed range of densities (Fig. 2.2.; panels a, b and c). The piecewise regression carried out for each of these three regions displayed a negative linear relationship between density and growth in each of the two density intervals (Fig. 2.2.; panels a, b and c). Assessment of Akaike weights showed that the model consisting of two different strengths of linear density dependence, operating over separate density intervals, explained the data better than a model assuming quadratic density dependence over all densities (Table 2.1.). Model MSEs were consistent with the model suitability found using Akaike weights, except in one region (OS grid reference SH) where the MSE was the same for both models (Table 2.1.). Out of the 3 regions in which negative quadratic density dependence was found, one region (OS grid reference SS) exhibited one

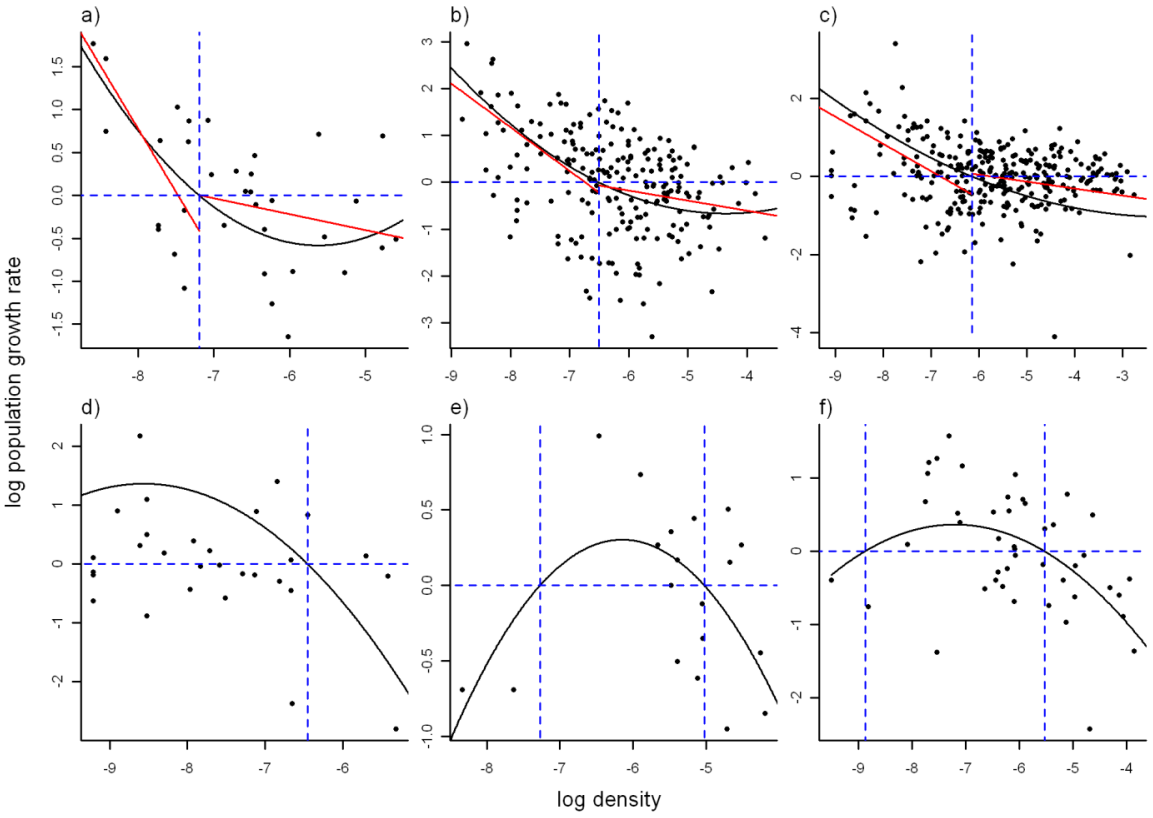

Fig. 2.2. Analysis of the six regions in which quadratic density dependence was found for *Ochlodes sylvanus*. Plots show the relationship between log per capita growth rate and log population density. Panels a)-f) correspond to regions with OS grid square references SH, SY, SO, SS, TG and SJ, respectively. Panels a)-c) show positive quadratic density dependence and d)-f) show negative quadratic density dependence, illustrated by the black line. Equilibria exist where the dashed blue lines cross. Red lines represent an alternative model where by two density-dependent processes occur at non-overlapping density intervals. d) displays a weak Allee effect. e) and f) display strong Allee effects.

Table 2.1. Table of model suitability scores for *Ochlodes sylvanus* populations within three regions displaying positive quadratic density dependence. These were the only populations to exhibit positive quadratic density dependence over all densities. Model 1 represents the effect of log quadratic density dependence on log per capita growth rate over all densities and model 2 represents log linear density dependence on log per capita growth rate at two non-overlapping density intervals. Model suitability is given by Akaike weight and mean square errors (MSE)

Region[a]	Model	Akaike weight	MSE
SH	1	0.29	0.43
	2	0.71	0.43
SY	1	0.35	0.97
	2	0.65	0.95
SO	1	0.00	0.90
	2	1.00	0.68

a: Region expressed as OS grid square references

equilibrium and two regions (OS grid reference TG and SJ) exhibited two equilibria (Fig. 2.2.; panels d, e and f).

The three weather factors most frequently affecting populations at the 100 km square scale were previous year spring rainfall, previous year autumn temperature and current year spring temperature. Previous year spring rainfall and previous year autumn temperature had a positive and negative relationship, respectively, with log per capita growth rate, in all regions in which they were significant factors. Current year spring temperature was negatively related to log per capita growth rate in six out of the seven regions in which it had an effect. All other weather variables were either influential in few regions, or had a mixture of positive and negative effects depending on the regions, or both.

The relative magnitude of effect of density dependence and weather was evaluated for the 17 regions in which both had a significant influence on population change. Analysis revealed a larger percentage increase in ML on elimination of density-dependent terms compared to the elimination of weather terms in 13 regions while weather caused a larger increase in four regions. The distribution of these regions is illustrated in Fig. 2.3. The mean percentage increase in ML across all seventeen regions due to exclusion of density dependence was 10.5% (SE = ± 2.1%; range = 2.3% to 37.3%) and the mean percentage increase in ML across all seventeen regions due to exclusion of weather factors was 7.4% (SE = ± 2.5%; range = 1.1% to 42.9%).

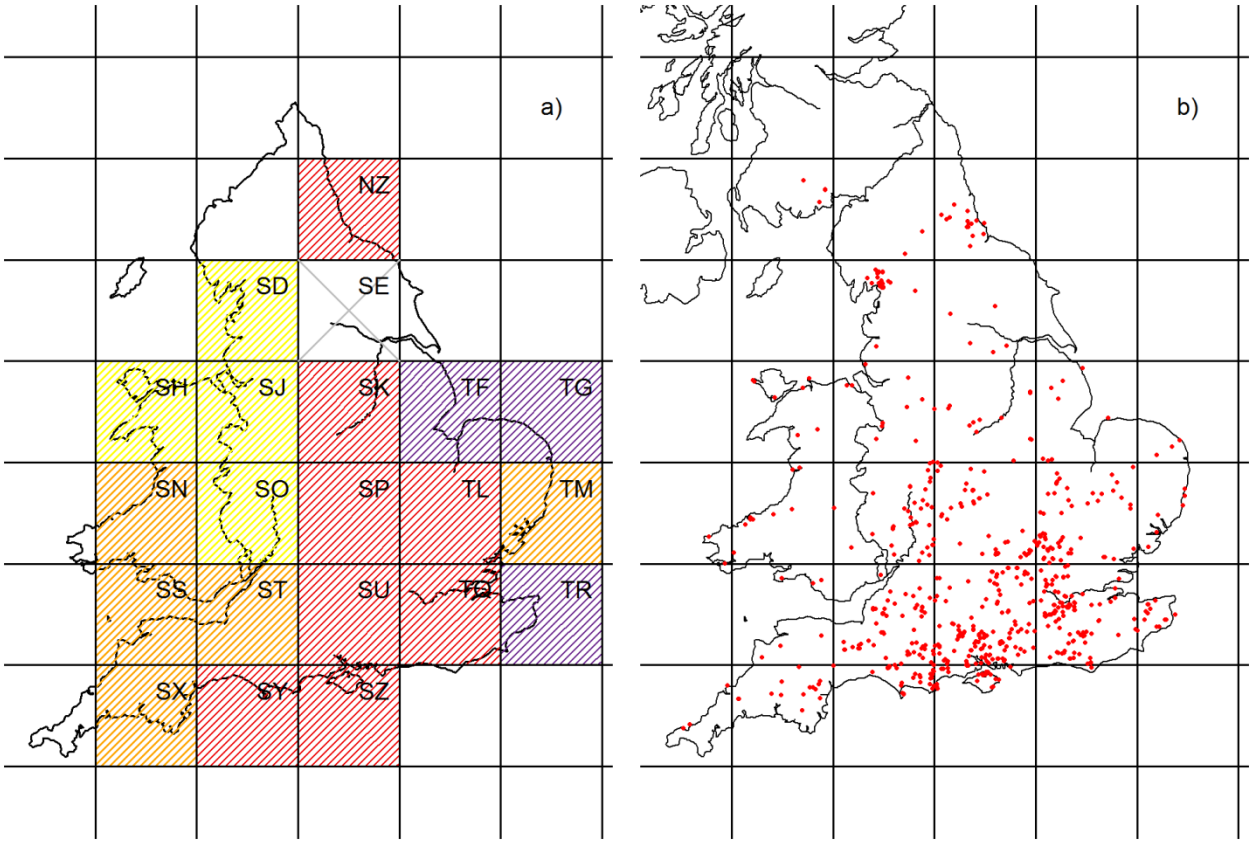

Fig. 2.3. a) Spatial distribution of factors influencing the population dynamics of *Ochlodes sylvanus* across its range. The OS grid reference of each 100 km square region is printed in the top right corner of the grid squares. Yellow squares show regions where density-independent weather factors were more influential; orange squares represent regions where density dependence was more influential (between 1.1 and 2 times more than weather); light red represent regions where density-dependence was more influential (>2 times more important); purple shows regions in which density dependence alone influenced population dynamics. The grey cross indicates the one region in which population dynamics were not significantly affected by any of the variables tested in this study. b) Spatial distribution of monitored sites across *Ochlodes sylvanus'* range.

2.4. Discussion

I have shown that qualitative spatial variation in density-dependent processes and density-independent drivers of population dynamics exists for *O. sylvanus*. The population dynamics of one out of the 21 100 km square regions analysed was not affected by either density or by any of the weather variables tested. All other regions displayed either linear or quadratic density dependence. In the 14 regions exhibiting linear density dependence the relationship between population change and density was consistently found to be negative, and never positive, corresponding to classical population regulation theory (Royama, 1992). I detected positive quadratic density dependence in three regions, each possessing a single equilibrium. After further inspection of the relationship between population growth and density within these regions, using model suitability scores, it was evident that the alternative model tested represented population dynamics more accurately. The alternative model consisted of two linear relationships (of differing strengths) between per capita growth rate and density, one where the population increases towards carrying capacity at low densities and one where it decreases towards carrying capacity at high densities. The two processes are illustrated in Fig. 2.2. a)-c) which shows that the population is regulated more strongly, i.e. driven towards carrying capacity more quickly, at lower densities compared to higher densities.

I identified three regions that displayed negative quadratic density dependence. One of these regions (OS grid reference SS) possessed a single equilibrium indicative of population regulation, and an overall relationship between growth and density that can be associated with weak Allee effects. Populations with weak Allee effects experience a reduction in per capita growth rate as smaller densities are reached, however, the per capita growth rate does not drop below 1 (log per capita growth rate does not drop

below 0), i.e. the population does not experience decline, just a lowered increase in growth (Fig. 2.2. d). By contrast, strong Allee effects do cause a population to decline at small densities, creating an unstable equilibrium with a corresponding 'critical density' below which the population is driven to extinction (Courchamp *et al.*, 2008). I found evidence for strong Allee effects in two regions (Fig 2. e) and f)). Allee effects are extremely difficult to detect due to the limitations associated with low density data (Kramer *et al*,. 2009) and this study highlights this point again. Caution should be taken when interpreting the findings presented here as in both regions displaying strong Allee effects few low densities were observed. Future analysis of longer time series for sites within these regions will allow a more robust assessment of Allee effects to be carried out. Because one of the main aims of this study was to identify spatial variation in both density dependence and density independent factors it was necessary to collate data and analyse populations at the 100 km square level. This may have caused site level Allee effects to go undetected, especially in regions with a large number of sites. To explore the potential existence of Allee effects for the large skipper I suggest site level analysis of long time series. Similarly, weather effects may operate at the site level and may have been undetected in this study. These potential differences in population dynamics at the site level may be due to the possibility of butterfly behaviours differing between the habitat types and habitat characteristics that vary between sites, as has been shown for the Fender's blue butterfly *Icaricia icarioides fender* (Schultz and Crone, 2001).

The identification of strong Allee effects alone may not be enough to evaluate extinction risks as density-dependent and -independent processes may interact. For example, a population that responds strongly to density-independent factors may be driven to densities below a 'critical density' frequently. The negative impact of density-

independent factors will then be amplified by the Allee effect increasing the risk of population extinction. Only one of the two regions displaying strong Allee effects was also influenced by weather. The coupled effect of weather and Allee effects could therefore be assessed by further studies that compare the risk of extinction for populations of *O. sylvanus* in each of these two regions.

I found that a variety of different weather factors affected the population dynamics of different regions. Previous year spring rainfall consistently proved to have a positive influence on population growth for all regions in which its effect was significant. This supports earlier research in which a positive impact of previous year spring rainfall was detected for *O. sylvanus* at the UK spatial scale (Pollard, 1988; Roy *et al*., 2001). Although this result is consistent with previous study, my results highlight the importance of additional weather variables for *O. sylvanus*, in particular previous year autumn temperature and current year spring temperature. My results also suggest that different weather variables may be important for *O. sylvanus* population dynamics in different regions across its British range. Analyses at a national level are likely to miss these local variations in influences and simply identify weather variables that have the strongest consistent effects across regions. These analyses may also be biased by a larger number of sites in the most well recorded regions.

Increased spring rainfall may lead to increased vegetative growth and therefore enhanced food availability for individuals in the late larval and adult stages of the large skipper life cycle. Stored larval nutrients along with adult nectar intake are important to reproductive potential (O'Brien *et al.*, 2004; Boggs & Freeman, 2005) which may result in increased fecundity and are possible explanations for increasing per capita growth rate with spring rainfall. Previous year autumn and current year spring temperature generally

had negative effects on population growth, implying that as temperature increases survival of the corresponding early larval and late larval/pupal stages of the large skipper's life cycle decreases. Larval survival has been shown to be directly influenced negatively by temperature in some insect groups, e.g. Varikou, 2009 (Thysanoptera: Thripidae) and Lysyk, 1998 (Diptera: Muscidae) (Lysyk, 1998; Varikou *et al.*, 2009). Singer & Parmesan (2010) highlighted the importance of phenological mismatches between Edith's checkerspot butterfly *Euphydryas editha* and its host plant, and similar phenological mismatches could potentially be a contributing factor to large skipper larval survival. Appropriate phenology studies for the large skipper butterfly could develop our understanding of larval survival under different temperature regimes.

Understanding weather effects is crucial for predicting how populations will be affected by climate change. My results suggest that, when evaluating how a species will respond to climate change, the consideration of spatially varying responses to certain weather variables is a central element. In addition, it should be noted that responses to extreme weather conditions may not be easily predicted from a study such as this. The results for the effects of winter temperature were inconclusive in terms of predictability, with per capita growth rate of two regions being negatively associated with winter temperature and three regions being positively associated with winter temperature. Crozier (2004) highlighted the importance of cold tolerance for *Atalopedes campestris*, a skipper butterfly common to South and North America, and found that population growth correlated positively with mean January temperature. This relationship may not have been consistently identified in this study due to extreme cold winter temperatures that are lethal to large skipper larval survival not being observed throughout the monitored sites over the whole time period I used. Additionally, extreme highs and lows in weather

variables may lead to quadratic weather effects playing a key role in population responses to climate change (McLaughlin *et al.*, 2002).

The population dynamics of three coastal regions in East England were only affected by population density and not by density-independent factors. All other regions (except one region in which no significant effects were found) were influenced by both. Density dependence had an effect of greater magnitude on population dynamics than weather factors in South-West, Central and North-East regions of its British range while density-independent factors appeared to be more influential on population dynamics in regions clustered in North Wales and North-West England (Fig. 2.3.). This spatial clustering suggests that a gradual switch between density dependence and density independence being more influential on population dynamics occurs as the range of *O. sylvanus* is crossed from East to North-West. At this spatial scale, however, I cannot draw any detailed conclusions about the existence of a spatial gradient. Repeating the analysis on a smaller spatial scale, e.g. 50 km square, would be necessary to investigate this further. Unfortunately, current sample size would cause gaps in the large skipper's range where analysis is not possible. While geographical gradients in the influence of density dependence and environmental covariates are sparse, they have been shown for some species (Cooke *et al.* 2012; Tkadlec & Stenseth, 2001; Saether *et al.*, 2008).

Understanding the combination of influential factors, and their combined effect, on population dynamics is necessary in choosing effective management strategies for different populations (Lockwood & Lockwood, 2008). I have shown that this combination of factors differs between regions for *O. sylvanus* and highlight the possibility that a similar pattern of spatial variation may exist for other Lepidoptera species. This is particularly important to threatened species as conservation actions may need to differ

between populations. For example, managing a population significantly affected by weather could be very different to managing one that is not affected by weather. Weather, as well as other density-independent factors, e.g. habitat management, may govern the overall availability of resources, such as nectar and larval host plant, within a population's habitat and may, therefore, control the position of equilibrium (the carrying capacity). The population may then be regulated by density to the position of equilibrium set by density-independent factors (Sinclair, 1989; Belovsky & Slade, 1995). As decreased carrying capacity has been correlated with extinction risk (Griffen & Drake, 2008) it is vital to understand how significant weather effects cause fluctuations in carrying capacities in different regions. In order to estimate a population's extinction risk the focus of further research should therefore be on the relative contribution of density-independent and density–dependent processes so that position of equilibria and strength of population regulation can accurately be assessed.

Chapter 3: Methodology development for the detection of Allee effects in British butterfly populations

3.1. Introduction

In the last chapter I detected Allee effects for the large skipper at the 100 km square scale in two regions within its British range. However, this may have been an underestimation of the presence of Allee effects for this species. Local population level Allee effects may have gone undetected if the majority of populations within a region are not subjected to Allee effects, masking the density-dependent relationship exhibited by the few populations exposed to Allee effects. In order to obtain better estimates for the prevalence of Allee effects for butterfly species, it is more appropriate to analyse population dynamics at the local population level. Many studies, like the large skipper analysis of Chapter 2, use classical (frequentist) statistics (Turchin, 1990; Woiwod & Hanski, 1992; Roy *et al.* 2001) to investigate population dynamics, but more recent studies have utilised Bayesian approaches (Hosack *et al.,* 2012; Gilroy *et al.*, 2012). Bayesian statistics are becoming more and more popular in the environmental and ecological sciences, especially those that utilise hierarchical Bayesian Frameworks as they allow the inclusion of a large number of variables, parameterisation of a large number of parameters and the partitioning of different forms of error (Clark 2005).

In this chapter, I developed a statistical approach for detecting Allee effects across multiple populations for which count data are available. I developed this approach by analysing multiple simulated population data sets. The simulated data sets were generated such that each included different forms of density dependence and different

forms of error. The ultimate aim is to apply this statistical approach to all British butterfly species so that their individual populations can be categorised by their form of density dependence. As in Chapter 2, I used quadratic and linear density-dependent models to test for different forms of density dependence in the population data. However, in this study, I specified the models as negative quadratic and negative linear, though pre-defined priors, to test for population regulation with and without Allee effects, respectively. I discuss the observation error associated with count data and their corresponding per capita growth rates, and explain how I used this knowledge to build appropriate hierarchical density-dependent models that account for observation error. Using my results I discuss and define an efficient and accurate methodology for detecting population level Allee effects in the UKBMS data in the following chapter.

3.2. Methods

3.2.1. Data Simulation

Time series data were generated for six populations, each representative of different density dependence and error regimes. All of the simulated populations were regulated towards an equilibrium population size (referred to as population regulation) and three of these were given additional Allee effect. Therefore, across the six populations there were two forms of density dependence: negative density dependence (indicative of population regulation) and negative quadratic density dependence (indicative of Allee effects). To mimic the dynamics of population regulation I used the Hassell density dependence equation (Hassell 1975):

$$x_t = x_{t-1}\left(\frac{\lambda}{(1+\gamma x_{t-1})^b}\right) \qquad \text{(Eq. 3.1.)}$$

where x_t is population density at year t, γ and b determine the relationship between mortality and population density, and λ is the maximum reproductive potential of an individual. γ scales the population to the population's carrying capacity and b characterizes population behaviour around the equilibrium. When 1≥b>0 the population will return to its point equilibrium and when 2>b>1 it will oscillate around its equilibrium, for large values of λ. As I wanted to avoid having populations with complex oscillatory behaviour I set b to 1. This allowed populations with varying degrees of stochasticity to be easily compared with one another without having to account for differing oscillatory behaviours. For the populations with additional Allee effects I used a modified form of Eq. 3.1. adapted from the Allee equation outlined in Fowler & Ruxton 2002:

$$x_t = x_{t-1}\left(\frac{(1-Ae^{-\gamma x_{t-1}})\lambda}{1+\gamma x_{t-1}}\right) \qquad \text{(Eq. 3.2.)}$$

where A is the strength of Allee effect.

Of the three populations in each of the two categories of density dependence, one was set to be non-stochastic, one stochastic and one stochastic with observer error. Non-stochastic populations were generated using Eq. 3.1. and Eq. 3.2. solely, and stochastic populations were generated with the inclusion an error term, ε_t.

$$x_t = f(x_{t-1}) + \varepsilon_t$$

where $f(x_t)$ is the function that governs density dependence (the right hand side of either Eq. 3.1. and Eq. 3.2.), and ε_t is the error term that was varied randomly with time by extracting a random value from a normal distribution with mean of 0 and standard deviation of σ at each time step. To emulate the time series found in the UKBMS data two more populations were created (one with an Allee effect and one with negative linear density dependence) by adding observation error to the stochastic populations. I did this by randomly selecting a new population size from a Poisson distribution with mean (and

variance) of the population density, at time t, from the corresponding stochastic population. All time series were created for a 50 year period.

As immigration was not incorporated into the simulated populations' dynamics, if a population went extinct recolonisation was not possible and the population remained extinct. In order to prevent populations with strong Allee effects from going extinct in just a few years I set the initial population density at year zero to be greater than the carrying capacity with a value of 50, and I set parameters γ and λ at 0.1 and 3, respectively. To prevent stochastic populations from going extinct quickly ε_t could not be too large but it also needed to be large enough to allow the creation of populations with relatively high stochasticity in order to mimic wild populations. This was done by selecting ε_t from a normal distribution with standard deviation σ equal to 3.

Three ecological models were fit to these simulated data sets in two model selection procedures: the first to identify whether the correct ecological model is selected in the absence of observation error and the second to identify whether the correct ecological model is selected in the presence of observation error. These two model selection procedures are described in the following two sections.

Analyses were carried out on simulated time series from year 1 until year 50 or the year of population extinction.

3.2.2. Model Selection: Ecological Process

The aim of this first model selection procedure was to assess whether the correct ecological processes present in the data were correctly detected. Here, I analysed non-stochastic and stochastic populations, by fitting the data to ecological models, which I will

refer to as candidate models, and carrying out model selection to assess model suitability of each candidate model for each simulated population. The candidate models were:

Model 1 $$Y_t = -\alpha_0 {X_{t-1}}^2 + \alpha_1 X_{t-1} + \alpha_2 + \omega;\ \alpha_0 > 0$$

Model 2 $$Y_t = -\alpha_1 X_{t-1} + \alpha_2 + \omega;\ \alpha_1 > 0$$

Model 3 $$Y_t = \alpha_2 + \omega$$

where,

$$Y_t = log\left(\frac{x_t}{x_{t-1}}\right) = X_t - X_{t-1};$$

$$\omega \sim \mathcal{N}(0, 1/\tau);$$

$$\tau \sim \text{Gamma}(10,1)$$

Y_t is log per capita growth rate, x_t and X_t are unlogged and logged population density, respectively, and ω is process error. α_0, α_1 and α_2 are parameters with priors of normal distribution except when they have a preceding minus sign, in which case the priors had gamma distributions. Model 1 has negative quadratic density dependence and is used to detect Allee effects. Model 2 has negative linear density dependence and is used to detect population regulation. Model 3 is the null model. The prior for τ restricts Y_t to realistic values whilst remaining relatively uninformative. Bayesian analyses were carried out to estimate model parameters and model deviance using WinBUGS version 1.4.3 and R version 2.15.2 (Lunn *et al.*, 2000; R Development Core Team, 2010). I used the 'bugs' function within the "R2WinBUGS" R package to allow WinBUGS outputs to be read into and analysed in R (Gelman *et al.*, 2013). Each run consisted of 10,000 iterations and 3 chains. The first half of iterations was discarded and to eliminate autocorrelation among a parameter's estimates within a chain, iterations were thinned so that every 3rd iteration was kept.

To check for parameter convergence I used the multivariate potential scale reduction factor (mpsrf) values (Plummer *et al.*, 2012) which provides a measure of the variance between chains compared to the variance within chains. When these two variances are similar, the chains have reached their target distribution. mpsrf scores less than 1.1 are indicative of chain convergence. To obtain mpsrf scores I first converted the WinBUGS output into the correct list format using 'convert.to.coda' function in the "adaptMCMC" R package (Scheidegger, 2012). I then used the 'gelman.diag' function in the "coda" R package to extract mpsrf values (Plummer *et al.*, 2012). If a mpsrf score was above 1.1 I re-ran the analysis of the non-converged candidate model increasing the number of iterations by 10,000 up to 200,000 iterations, stopping when convergence was achieved. Model suitability can be measured by deviance or the Deviance Information Criterion (DIC). DIC is the Bayesian equivalent of Akaike Information Criterion (AIC) and is calculated by the deviance (measure of model fit) plus the 'effective' number of parameters (pD), i.e. DIC is a penalised likelihood approach (Spiegelhalter, 2002; Lunn *et al.,* 2013) that penalises models with higher complexity. Informative priors define the parameter space from which the parameter should be estimated and therefore restricts the freedom of parameters. This causes the number of parameters to be less obvious and so an 'effective' number of parameters is estimated in order to calculate a model's DIC (Spiegelhalter, 2002; Lunn *et al.* 2013). The DIC, pD, deviance and mpsrf scores for each model were recorded for each data set.

3.2.3. Model Selection: Observation Error

The second model selection procedure was carried out to evaluate whether the inclusion of observation error in candidate models would aid detectability of ecological processes.

The UKBMS estimated site level abundances are count data and their associated error structure has a Poisson distribution. Population densities are scaled counts and their associated error structure has similar shape to that of Poisson distributions but differs in that densities may take non-integer values. For this reason I assigned a gamma distribution to the population density error structure, with *shape =* x_t *(unlogged population density)* and *rate = 1* to emulate the shape of corresponding Poisson distributions. This is shown for three example densities 1.0, 2.0 and 10.0 in Fig. 3.1. a), c) and e), respectively. The distributions of these densities logged are shown in Fig. 3.1. b), d) and f) to illustrate how the error distributions in population density translate into the error distributions of log population density, the explanatory variable in all of my candidate models. For the purpose of comparing Poisson and gamma distributions in Fig. 3.1. I have added 1 to x_t (unlogged population density) before taking logs because sampling from a Poisson distribution produces zeros. For my analyses it was not necessary to include this plus 1 in the candidate models as sampling from a gamma distribution produces only values greater than 0. Using a gamma distribution was also advantageous to the model selection procedure as it facilitated the calculation pD and DIC which would not have been possible had I used discrete parameters produced by the Poisson sampling (Lunn *et al.*, 2013, page 163).

To assess the error structure of observed log per capita growth rate Y_t^{obs} I sampled from two Poisson distributions, one representing a count at time t and the other represented a count at time t-1, and calculated the corresponding true log per capita growth rate Y_t^{true} 100,000 times to create the distribution of Y_t^{true} representing the error distribution of Y_t^{obs}. The error structure of the log per capita growth rates were found to be normally distributed around the sample mean with standard deviation that varied with

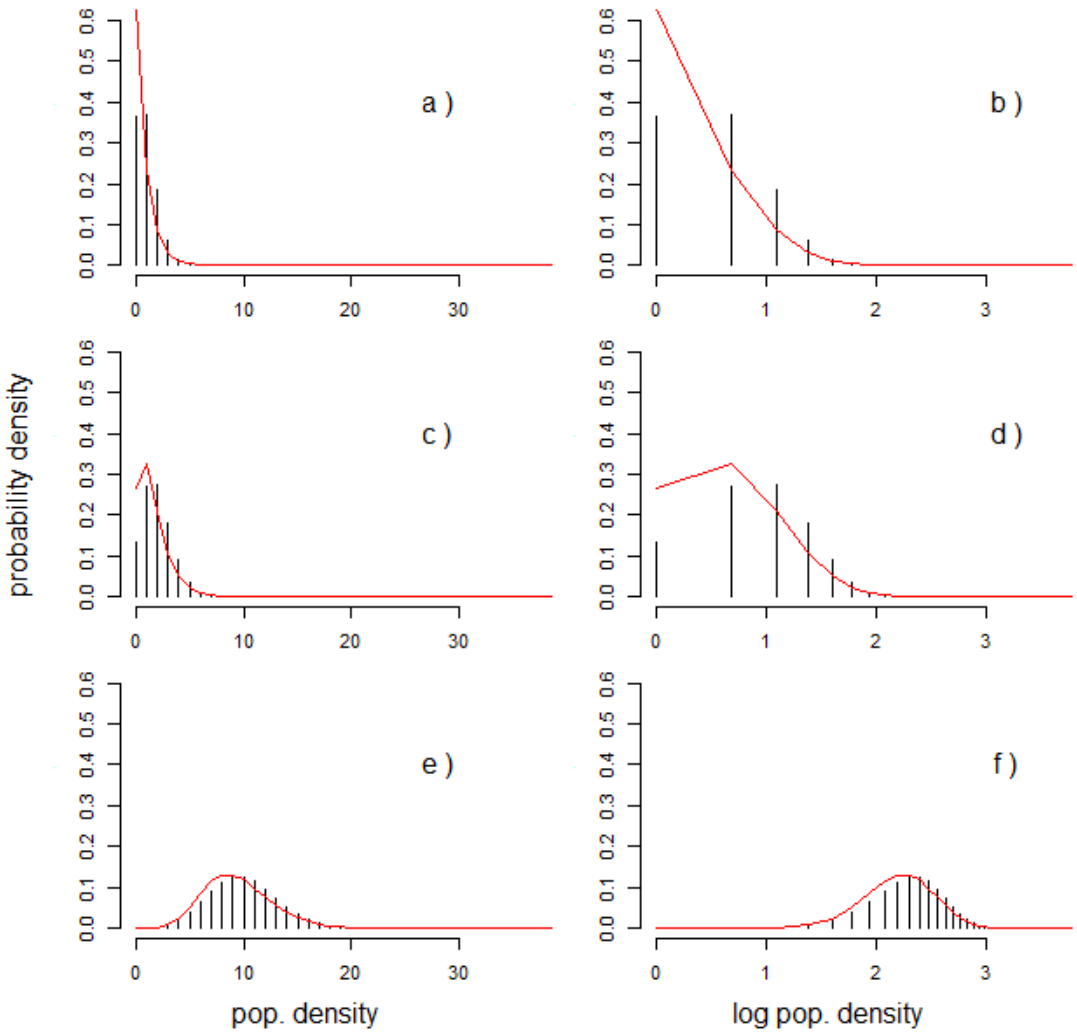

Fig. 3.1. Error distributions for population densities a) 1.0, c) 2.0 and e) 10.0, and corresponding error distributions for the log of these population densities b), d) and f), respectively.

x_t (unlogged population density at time t) and x_{t-1} (unlogged population density at time t -1) as shown in Fig. 3.2. Note that ${Y_t}^{obs}$ is the same when calculated from counts or densities x_t (as the area scalar for x_t and x_{t-1} cancels out) and it is more efficient here to use the Poisson distributions associated with counts rather than the Gamma distributions associated with unlogged population densities x_t so that fewer error structures need to be assessed; the subset of UKBMS data I analyse in the next chapter contains 1,557 unique counts but 16,339 unique densities.

Using the above information I constructed a model that incorporated observation error in observed log per capita growth rate (${Y_t}^{obs}$) and unlogged observed population density at time t -1 (${x_{t-1}}^{obs}$):

$$ {x_{t-1}}^{true} \sim Gamma({x_{t-1}}^{obs}, 1) $$

$$ {Y_t}^{true} = f\left({X_{t-1}}^{true}\right) + \omega $$

$$ {Y_t}^{obs} \sim \mathcal{N}\left({Y_t}^{true}, {\sigma_t}^2\right) $$

where standard deviation σ_t is calculated as described above using the counts at time t and t-1. I fitted models with and without errors in ${Y_t}^{obs}$ and ${x_{t-1}}^{obs}$ to stochastic simulated populations that included observation error. I did this for the three $f(X_{t-1})$ (candidate models 1-3), to evaluate whether incorporating observation error was beneficial to detecting the correct form of density dependence. The same model selection procedure as in 3.2.2. was used here.

3.2.4. Application to UKBMS Data

The UKBMS data contains more than 5000 populations that are unique in species and location (site), and have 10 or more pairs of consecutive years of counts between 1974 and 2011. Because of the large number of populations it is essential to develop a highly

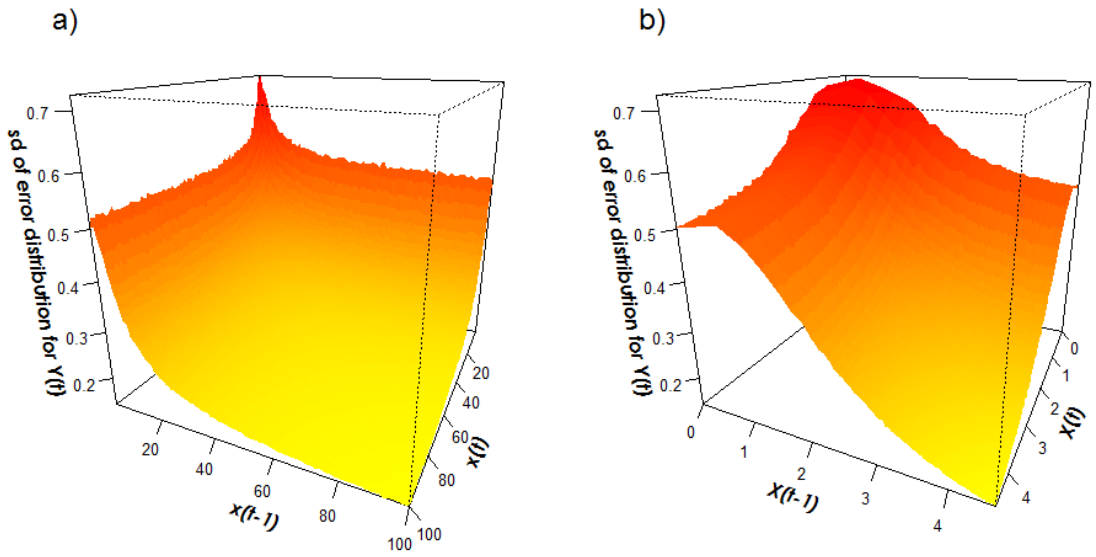

Fig. 3.2. 3D plots to show how standard deviation of the normally distributed error in observed log per capita growth rate (Y_t^{obs}) varies with a) unlogged population density at time t (x_t) and t-1 (x_{t-1}), and b) logged population density at time t (X_t) and t-1 (X_{t-1}).

efficient method, but such a large data set captures a large variation in time series characteristics across populations, and therefore it's important to ensure that efficiency is achieved without compromising the accuracy of the results. The candidate models that account for errors in observed log per capita growth rate (Y_t^{obs}) and unlogged observed population density at time t-1 (x_{t-1}^{obs}) are complex and very computationally intensive. To reduce model complexity, and therefore computation time, I considered the necessity of including errors in both Y_t^{obs} and x_{t-1}^{obs}. I did this by evaluating how the error distributions in Y_t^{obs} and x_{t-1}^{obs} varied with x_{t-1}^{obs} (and, more precisely, X_{t-1}^{obs} - the logged observed population density at time t-1), to guide the construction of new models of reduced complexity.

3.3 Results

3.3.1 Data Simulation

Data sets for six simulated populations were generated. Their associated time series are shown in Fig. 3.3. and growth plots in Fig. 3.4. All three populations without an Allee effect survived for the full 50 years, and populations with an Allee effect went extinct at years 20, 27 and 27 for the non-stochastic population, stochastic population and stochastic population with observation error, respectively.

3.3.2. Model Selection: Ecological Process

All candidate models converged (mpsrf ≤ 1.1) for non-stochastic and stochastic data sets containing Allee effects by 10,000 iterations. However, by 200,000 iterations the negative quadratic candidate model had not converged for the two data sets absent of an Allee effect and the negative linear candidate model had not converged for the data set absent

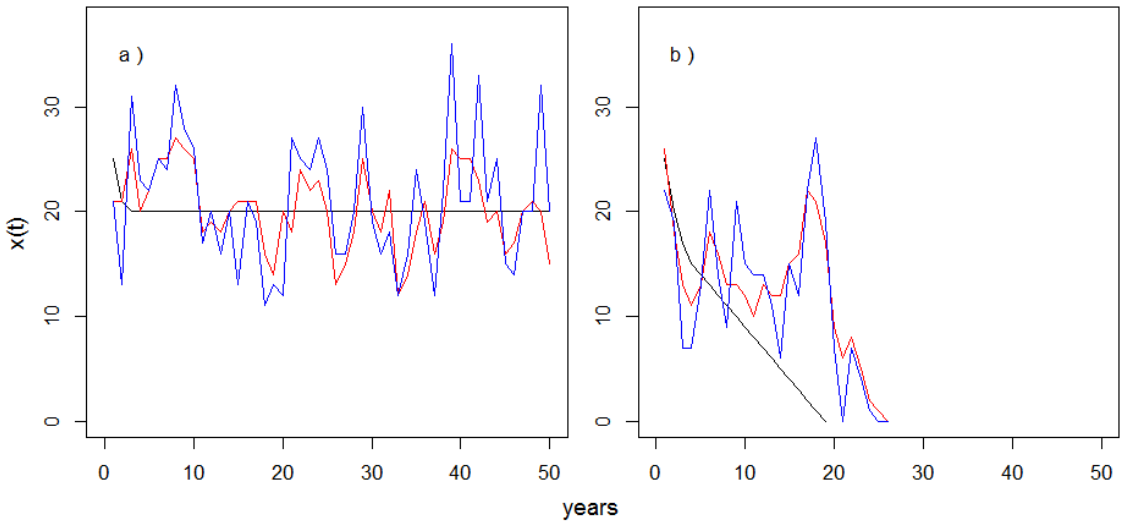

Fig. 3.3. Time series of six simulated populations. Plot a) displays regulated populations and plot b) displays regulated populations also influenced by Allee effects. Black, red and blue lines represent non-stochastic populations, stochastic populations and stochastic populations with unlogged densities, x_t, inclusive of observation error, respectively.

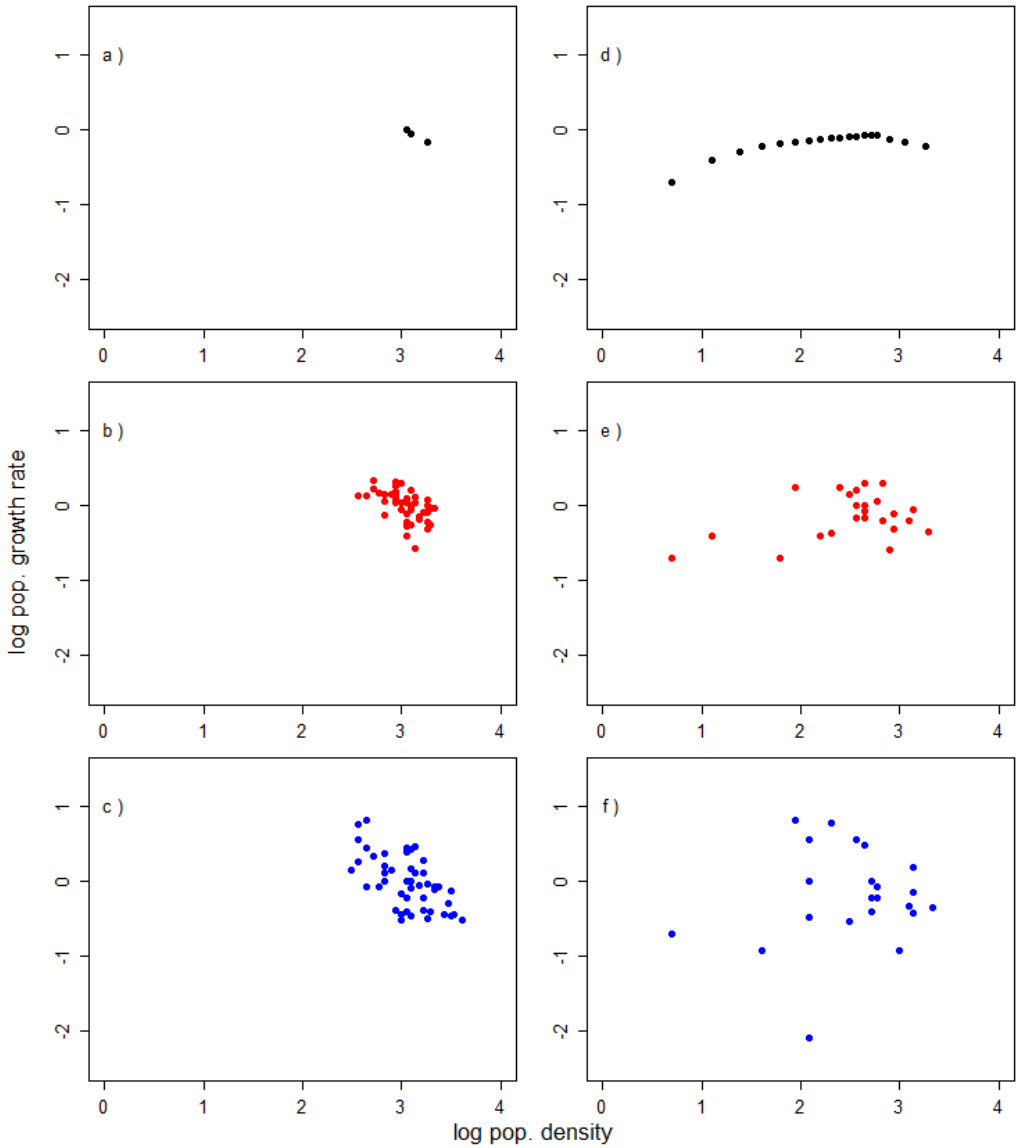

Fig. 3.4. Population growth *vs* log population density. a)-c) plots display regulated populations and d)-f) plots display regulated populations also influenced by Allee effects. Plots with black, red and blue dots represent non-stochastic populations, stochastic populations and stochastic populations with log population densities, X_t, inclusive of observation error, respectively.

of both stochasticity and an Allee effect. Convergence was achieved by 20,000 iterations for all other models fitted to data absent of an Allee effect. Models with lowest DIC and lowest deviance for each data set are highlighted in bold in Table 3.1. For the stochastic data set without an Allee effect the negative linear model had DIC and deviance more than 5 lower than those for the null model. The model with lowest DIC for data sets containing Allee effects was the negative quadratic model, which was only 4.86 and 2.92 lower than the model with the next lowest DIC (the null model) for non-stochastic and stochastic data sets, respectively. The deviance for the NQ model was 6.71 and 5.01 lower than the next lowest deviance (that of the null model) for non-stochastic and stochastic data sets, respectively, as shown in Table 3.1.

3.3.3. Model Selection: Observation Error

The two simulated data sets analysed in this model selection procedure possessed both stochasticity and observation error; one with and one without an Allee effect. The model with lowest DIC for the data set without an Allee effect was the less complex negative linear model in which observation error was not accounted for, whereas the model with lowest deviance, for this data set, was the negative linear model with observation error accounted for (Table 3.2). For the data set with an Allee effect the negative quadratic model with observation error had the lowest DIC and deviance. One model in this model selection procedure took 100,000 iterations before convergence was achieved, as indicated in italics in Table 3.2, all other models converged at 10,000 iterations.

The estimated number of model parameters was larger for all models containing observation error when tested on the longer time series data of the population without an Allee effect than on the shorter time series of the population with an Allee effect. This

Table 3.1. Candidate model statistics for the ecological process model selection procedure when tested on non-stochastic and stochastic simulated data sets. – indicates that the model did not converge within 200,000 iterations. NQ = negative quadratic density dependence. NL = negative linear density dependence. Null = no density dependence, i.e. the null model. Stoch = Stochasticity.

	Data											
	No Allee, No Stoch.			No Allee, Stoch.			Allee, No Stoch.			Allee, Stoch.		
Model	DIC	pD	dev	DIC	pD	dev	DIC	pD	dev	DIC	pD	dev
NQ	-	-	-	-	-	-	**-11.61**	3.38	**-14.99**	**9.16**	3.69	**5.47**
NL	-	-	**-**	**-25.60**	2.53	**-28.52**	-4.56	1.52	-6.12	14.08	1.71	12.37
Null	**-77.63**	1.72	**-79.35**	-16.51	1.72	-18.23	-6.75	1.53	-8.28	12.07	1.59	10.48

Table 3.2. Candidate model statistics for the observation error model selection procedure when tested on stochastic simulated data sets that included observation error. Italics indicate that the model converged between 20,000 and 200,000 iterations. NQ = negative quadratic density dependence. NL = negative linear density dependence. Null = no density dependence, i.e. the null model. Stoch = Stochasticity. Y_t is observed log per capita growth rate and x_t is observed unlogged population density.

	Data					
	No Allee, Stoch. + Obs. Error (N=49)			Allee, Stoch. + Obs. Error (N=25)		
Model	DIC	pD	dev	DIC	pD	dev
Including Error in Y_t^{obs} and x_t^{obs}						
NQ	*34.11*	*24.67*	*9.43*	**39.74**	12.68	**27.06**
NL	33.49	24.43	**9.06**	40.17	10.76	29.41
Null	38.13	23.00	15.13	40.20	10.38	29.82
Excluding Error in Y_t^{obs} and x_t^{obs}						
NQ	17.74	2.77	14.98	51.82	3.19	48.63
NL	**17.70**	2.86	14.84	51.73	1.84	49.89
Null	38.13	1.72	36.41	50.54	1.59	48.95

is due to the former data set having more Y_t^{true} and x_{t-1}^{true} values to estimate than the latter data set. To evaluate whether time series length influenced the outcome of the model selection procedure I repeated the analysis on the final 25 years of the time series for the population without an Allee effect. The results of this auxiliary analysis show a similar pattern to those for the full time series of 49 years, with both the negative quadratic and negative linear models without observation error having lower DIC values than both the negative quadratic and negative linear models with observation error (Appendix B, Table B.1.).

The maximum difference between any two corresponding X_{t-1}^{obs} and X_{t-1}^{true} values and any two corresponding Y_{t-1}^{obs} and Y_{t-1}^{true} values estimated by the negative linear model for the data set with no Allee effect was 0.13 and 0.34, respectively, and the maximum difference between any two corresponding X_{t-1}^{obs} and X_{t-1}^{true} values and any two corresponding Y_{t-1}^{obs} and Y_{t-1}^{true} values estimated by the negative quadratic model for the data set with an Allee effect was 0.28 and 1.36, respectively.

3.3.4. Application to UKBMS Data

Because the candidate models that account for errors in observed log per capita growth rate (Y_t^{obs}) and unlogged observed population density at time t-1 (x_{t-1}^{obs}) are complex and very computationally intensive, I assessed the necessity of including such errors. I did this by evaluating how the error distributions in Y_t^{obs} and x_{t-1}^{obs} varied with x_{t-1}^{obs} (and, more precisely, X_{t-1}^{obs} - the logged observed population density at time t-1). Fig. 3.5. shows how the standard deviation of the error distribution of X_{t-1}^{obs} varies with X_{t-1}^{obs}, for the range of population densities found in the UKBMS data. Fig. 3.6. illustrates how the inclusion of errors impacts the results of two different simulated data sets. Using these

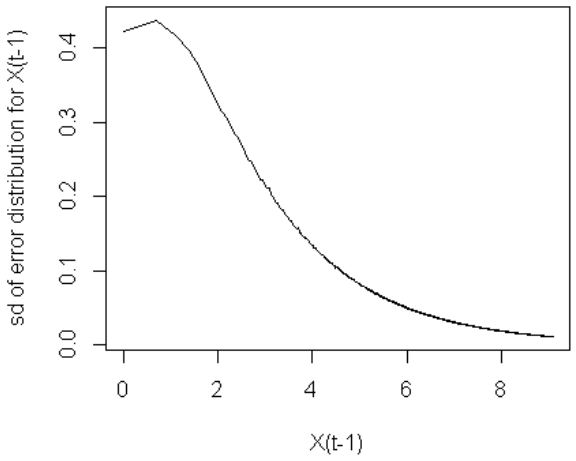

Fig. 3.5. The relationship between standard deviation of the error distribution of logged population density X_{t-1} and logged population density X_{t-1}.

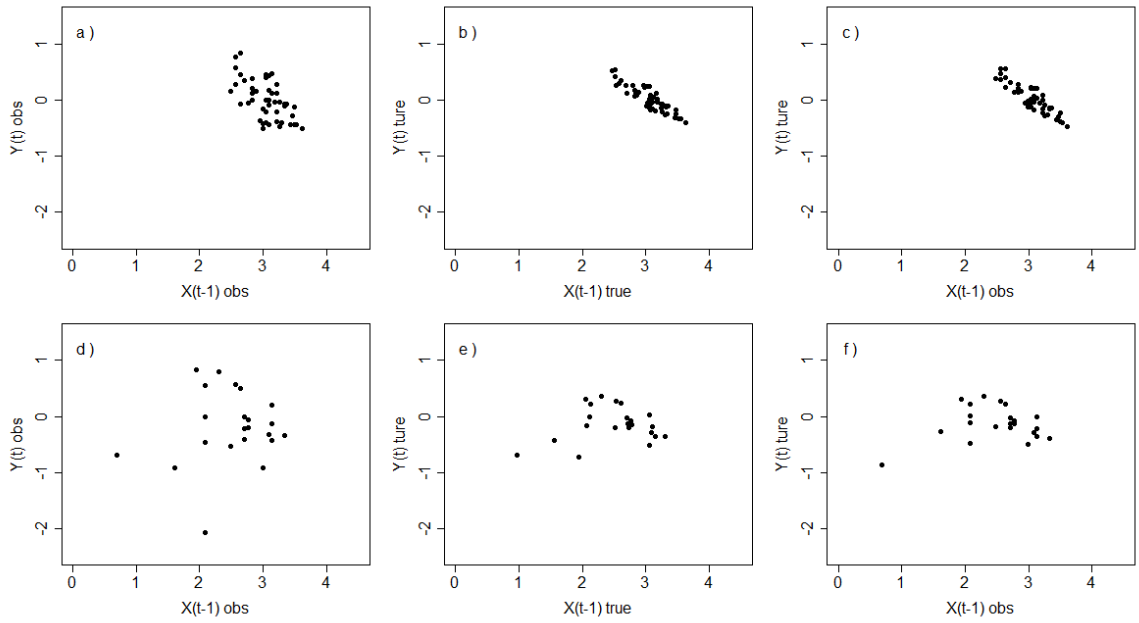

Fig. 3.6. Observed values of Y_t and X_t, and true values of Y_t and X_t estimated by different observation models for simulated data absent of an Allee effect and inclusive of observation error (a-c) and simulated data inclusive of both an Allee effect and observation error (d-f). a) and d) show observed values. b) and e) show values estimated by a negative linear and a negative quadratic model, respectively, both of which accounted for errors in both Y_{t-1}^{obs} and X_{t-1}^{obs}. c) and f) show Y_{t-1}^{true} values estimated by a negative linear and a negative quadratic model, respectively, both of which accounted for errors in Y_{t-1}^{obs} alone .

results I discuss the appropriate candidate models to be fitted to the UKBMS data in Chapter 4.

3.4. Discussion

Allee effects and population regulation were correctly detected in the simulated stochastic populations, in the initial model selection procedure that did not consider observation error. The Allee effect was also successfully selected for the non-stochastic simulated population. The negative quadratic model failed to converge for the stochastic population absent of an Allee effect, i.e. parameterisation of an Allee effect was not possible. This suggests that the negative quadratic model was unsuitable for describing the relationship between per capita growth rate and population density. The population with no stochasticity and no Allee effect reached its equilibrium population density in year 4 and therefore had a very small range in density fluctuations over the 50 year period, as seen in Fig. 3.3. This meant that the relationship between per capita growth rate and population density (Fig. 3.4.) was difficult to assess and explains why inference for models containing density dependence was not possible for this simulated population.

The inclusion of observation error in observed log per capita growth rate Y_t^{obs} and unlogged observed population density x_{t-1}^{obs} aided the detection of Allee effects when observation error was present in the data. Model selection for the population with observation error but without an Allee effect favoured the negative linear model that did not account for observation error. The negative linear model that did account for observation error had the lowest deviance for this population, as expected, as the additional parameters allow a better fit of the model to the data (Fig. 3.6. a and b). The DIC value of this negative linear model was 0.62 lower than that of the negative quadratic

model that accounted for observation error, whereas the DIC of the negative linear model without observation error was only 0.04 lower than that of the negative quadratic model without observation error. The larger similarity in DIC values for models absent of observation error could be due to the observation error present in the data being falsely detected as density dependence processes. From Fig. 3.6. a) it is clear that either negative linear or negative quadratic density dependence could be feasible representations of the data if observation error is not considered. When only the final 25 years of this time series data was analysed (Appendix B, Table B.1.) an incorrect model was selected, with the negative quadratic model without observation error being favoured. Although, when observation error was accounted for the negative linear model was correctly selected over the negative quadratic and null models. These results suggest that, in fact, inclusion of observation error into the density dependence models is beneficial to detecting the correct form of density dependence, and highlight the risk of obtaining misleading results when observation error is erroneously omitted, as shown in previous studies by Calder *et al.* 2003.

But why do the models with observation error have lower DIC than the models without observation error for the data set containing an Allee effect and not for the data set absent of an Allee effect? The answer lies in the extent to which a model is improved by adding extra parameters. As DIC is the deviance plus the effective number of model parameters, an increase in effective number of model parameters of one would need to be offset by a decrease in deviance of more than one to make the extra parameter worthwhile. Table 3.1. shows that this is the case for the population with an Allee effect but is not the case for the population without an Allee effect. This can be explained by considering the maximum difference between corresponding values of the logged

observed population densities X_{t-1}^{obs} and X_{t-1}^{true} and between corresponding values of the observed log per capita growth rates Y_{t-1}^{obs} and Y_{t-1}^{true} values which were higher for the population with an Allee effect compared to the population without. The small perturbations of true values from observed values for the latter population indicates that the inference of the density dependence part of the model was not improved (at least not to a great extent) by additional parameters at a different level of the hierarchical model, and therefore their inclusion was not worthwhile. The larger perturbations for the population with an Allee effect were due to the larger observation error present in the data needing to be accounted for. These larger errors in Y_{t-1}^{obs} and X_{t-1}^{obs} can be easily explained by their associated X_t^{obs} and X_{t-1}^{obs} values, as shown in Fig. 3.2. and 3.5.

Models that include observation error in both Y_{t-1}^{obs} and X_{t-1}^{obs} are computationally intensive and take a long time to run, which is not ideal for analysing over 5000 wild butterfly populations. I overcame this by taking advantage of the knowledge I had about the error distributions of X_{t-1}^{obs}. As relatively small errors in X_{t-1}^{obs} are associated with large X_{t-1}^{obs} it is sensible to assume that populations with no 'small' densities will benefit very little by including errors in X_{t-1}^{obs} and therefore a model with errors in Y_{t-1}^{obs} alone should be sufficient for these populations. The minimum log population density for the simulated population without an Allee effect was 2.48 (Fig. 3.6. a), and the maximum difference between corresponding X_{t-1}^{obs} and X_{t-1}^{true} values estimated by the negative linear model with errors in both Y_{t-1}^{obs} and X_{t-1}^{obs} for this population was only 0.13 (Fig. 3.6. b). Therefore, it is understandable that the negative linear model with errors in Y_{t-1}^{obs} alone inferred a very similar pattern in density dependence to the model with both forms of error, as illustrated by the similarity between Fig. 3.6. a) and b). By contrast, the minimum log population density for the

population with an Allee effect was 0.69 (Fig. 3.6. d)) and the corresponding X_{t-1}^{true} of this minimum X_{t-1}^{obs} value was 0.28. The exclusion of errors in X_{t-1}^{obs} for this population consequently led to quite a different pattern in density dependence, especially for the seven X_{t-1}^{obs} values <2.1, as shown in Fig. 3.6. e) and f). This suggests observation error in both Y_{t-1}^{obs} and X_{t-1}^{obs} should be incorporated into models when analysing populations with 'small' X_{t-1}^{obs} values to avoid misleading results, but for populations with only 'large' X_{t-1}^{obs} values it is appropriate to use the less computationally intensive models that only incorporate observation error in Y_{t-1}^{obs}, as this is unlikely to compromise results.

For the empirical analysis of all UKBMS populations (Chapter 4) 'small' X_{t-1}^{obs} will be considered as < 2.16 as the standard deviation of associated error distributions is ≤ 0.3. Without evaluating the impact of error sizes on a large number of simulated populations this cut off is always going to be slightly arbitrary, but a standard deviation of 0.3 is relatively small compared to the possible standard deviation of error distributions for Y_{t-1}^{obs} (Fig. 3.2.) and relatively small compared to the standard deviation of X_{t-1}^{obs} values greater than 2.16 (Fig. 3.5.).

Chapter 4: Allee effects in wild British butterfly populations: detection and attributing species traits

4.1 Introduction

Allee effects have been shown to occur in many different taxonomic groups through a number of independent studies (e.g. plants: Cappuccino 2004; insects: Menedez *et al.* 2002; birds: Soutullo *et al.* 2006; mammals: Mooring *et al.* 2004). However, the prevalence of Allee effects across species and across a given species' populations has received very little attention. Kramer *et al.* (2009) raises the point that Allee effect studies may select and investigate species/populations for which Allee effects are already suspected, for example invasive species (Liebhold & Bascompte 2003) or endangered species (e.g. Glanville fritillary *Melitaea cinixia*: Kuussaari *et al.* 1998). Comparative studies in which the commonness of Allee effects is addressed would allow the following questions to be addressed:

- Are Allee effects widespread across species?
- Are certain species more susceptible to Allee effects? If so, can we use this knowledge to ask questions about why different species are more susceptible to Allee effects than others?

In chapter 2 I examined the spatial patterns of density dependence for the large skipper *Ochlodes sylvanus* and found evidence of Allee effects at the 100 km square scale in certain regions of the large skipper butterfly's range. However, detecting Allee effects at this spatial scale may lead to an underestimation of their occurrence as any population

level Allee effects contribute only partly to the inference made at the regional level. The spatial scale used in chapter 2 was selected to ensure that enough data were available within a region to satisfy the minimum statistical power required when applying frequentist statistical methods. Population level analyses would only have been possible had I not included weather variables, important extrinsic drivers of butterfly population dynamics, or had I only used populations with more than 15 pairs of consecutive years of data, which would have reduced the number of populations included in the analysis greatly. In chapter 3 I developed a Bayesian framework that can be used to test for density dependence whilst incorporating weather (and any other density-independent factors influencing population dynamics) as process error. Another advantage to using this Bayesian framework is that observation error can be included into the analysis. Accounting for errors in observed data is paramount if a comprehensive examination of density dependence is to be achieved (Clark & Bjornstad 2004; Freckleton *et al.* 2006). In this chapter I apply the methodology developed in chapter 3 to categorise populations of 38 British butterfly species in terms of their density dependence. I use these categorisations to compare the prevalence of Allee effects within and between species.

Previous studies have identified three mechanisms driving Allee effects in butterfly populations: reduced mating (Glanville fritillary *Melitaea cinixia*: Kuussaari *et al.* 1998; Gypsy moth *Lymantria dispar*: Liebhold & Bascompte 2003; *Parnassius clodius* and *P. smintheus*: Calabrese *et al.* 2008), dispersal (Glanville fritillary *Melitaea cinixia*: Kuussaari *et al.* 1998) and lowered cooperative defence (Monarch *Danaus Plexippus*: Calvert *et al.* 1979). The latter was shown for the Monarch butterfly *D. Plexippus* in its overwintering sites in Mexico where avian predation increased with decreased colony size. To my knowledge there have been no reports of aggregations to avoid predation in

British butterflies, instead mate limitation and dispersal are the more likely drivers of Allee effects. Reduced mating arises because the probability of females successfully mating and producing healthy offspring decreases with population density (Tcheslavskaia *et al.* 2002), and this then results in a lowered reproductive output of the population and decreased per capita growth rate. Dispersal induced Allee effects may occur because a lack of conspecifics may indicate poor habitat quality (which may in fact include lack of mates). This may result in increased dispersal of individuals away from a population of low density, as was found for the Glanville fritillary *Melitaea cinxia* (Kuussaari *et al.* 1996). The ability of individuals to disperse from one habitat patch to another is influenced by a number of contributing factors, such as the mobility of a species and connectivity of patches (Hanski *et al.* 2004; Cowley *et al.* 2001). In this chapter I examined the influence of species mobility on the susceptibility to Allee effects with the prediction that increased species mobility will increase susceptibility to Allee effects. To select appropriate species traits that may be related to mate-finding Allee effects I first considered how butterfly mating strategies may increase the probability of finding mates.

Allee effects may go undetected for a species whose individuals do not reduce in fitness when densities become low, i.e. an individual's fitness does not benefit from forming groups. In this case the species may thrive at low densities (for example, due to increased resources, such as food plants, per individual) and all its populations should not exhibit Allee effects. A species that does benefit from its individuals forming groups may aggregate on a finer scale (finer than population level) to prevent Allee effects from occurring, e.g. by increasing the probability of finding suitable mates. In this case Allee effects would be present in some low density populations, for example due to aggregation not occurring frequently enough or with a large enough number of

individuals to prevent an Allee effect. For species that are susceptible to Allee effects, susceptibility may therefore vary with aggregating strategies employed to find mates. An example of an aggregated mating strategy is the formation of leks (Alcock, 1987). Leks are territories that females visit exclusively for mating and are absent of limiting resources (such as nectar and host plants) to females. These territories are set up at distinctive physical landmarks and attract numerous males. Accounts of leks have been documented for three species included in this study: the purple hairstreak *Neozephyrus quercus*, the large skipper *O. sylvanus* and the small heath *Coenonympha pamphilus* (Dennis & Williams 1987; Wickman 2009; Dennis 2010). Statistically, it is impossible to infer using a comparative analysis the influence of lekking on susceptibility to Allee effects when only three out of the 38 species included in this study employ this mating strategy. Leks are an example of a non-resource based aggregated mating system because the aggregations occur at physical landmarks (Wickman, 2009). Aggregated mating systems can also be resource based (Wickman & Rutowski 1999). Wickman (2009) provides a number of examples of resource based aggregations, e.g. *Lycaena hippothoe* males defending nectar plants needed by females, but highlights that few studies explicitly address their direct influence on mating success. As there is no comprehensive data on aggregated mating systems across British butterfly species, other than leks, I instead consider mating location sites that are associated with aggregated mating systems on the grounds that species known to utilise these sites may adopt beneficial gregarious behaviours that reduce their susceptibility to Allee effects. These mating location sites include nectar and host plant sites which are associated with resource based aggregated mating systems, and physical edge sites which have been identified as aggregation sites (Dennis 2010 pp. 83). Physical edge sites are zones between differing habitat types and have the potential

to promote an aggregated mating system in those species that use them as mating locations. Assuming that the use of nectar plant, host plant and physical edge sites increases a species' ability to engage in aggregated mating strategies, I predict that species utilising these sites will be less susceptible to Allee effects.

In addition to mating location sites, mate-location behaviour may play a role in a species' susceptibility to Allee effects. Alcock & O'Neill (1986) showed that male grey hairstreak *Strymon melinus* butterflies switched from territorial perching to patrolling as population density increased, and Wickman (2009) suggested that this was due to patrolling, where individuals search for mates during flight, in high density populations having a greater probability of finding and therefore mating females before they reach any territories where males perch waiting for mates to approach. In lower densities it may be beneficial for males to adopt territorial perching as territories are often associated with female resources and females will therefore seek out these territories if not intercepted by other males on their way. Because of this relationship between mate-locating behaviour and population density I hypothesise that species that engage in perching behaviours may have a lowered susceptibility to Allee effects as they may be able to respond more effectively to a reduction in mates compared to patrolling-only species.

Species are related through hierarchically structured phylogeny and are therefore non-independent due to their evolutionary history (Felsentein, 1985). Comparative analyses that investigate the effect of species traits on a response variable may lead to misidentification of significant effects if phylogeny is not taken into account, even though among species of similar lineage no significant trait effects are present. In this study I

account for phylogeny when analysing the influence of species traits on susceptibility to Allee effects.

4.2 Method

4.2.1 Butterfly Data and Bayesian Analysis

I extracted population data for all non-migratory species found in Britain from the UK Butterfly Monitoring Scheme (UKBMS) database. Migratory species, *Colias croceus, Vanessa atalanta and Vanessa cardui*, were omitted from the analysis as annual population densities result mainly from individuals migrating from Europe and North Africa rather than being populated by offspring of the previous year's inhabitants (Pollard *et al.*, 1984; Pollard & Greatorex-Davies, 1998; Stefanescu *et al.*, 2013). The UKBMS database consists of data collected by volunteers who monitor fixed-route transects through sites following the guidelines outlined in Pollard & Yates (1993). In this study I used the annual indices of abundance, estimated by UKBMS team, from 1971 to 2011 to calculate growth rates from one year to the next for each monitored site for each species. To avoid confusion I will refer to an individual monitored site for a given species as a population. Data corresponding to a previous year population density of zero were excluded as a zero density in the previous year can only be followed by the population remaining extinct or a recolonisation event due to immigration in the current year. As recolonisations are not a focus of this study I exclude them in order to assess density dependence accurately at low densities. Next I eliminated any populations for which less than 10 growth rates were calculated, and only analysed species with more than 10 populations that met this criteria. I converted all indices of abundance into densities by dividing the indices by the transect area of the corresponding population.

I used the Bayesian method outlined in chapter 3 to test for three ecological processes in each individual population. The three ecological processes are Allee effects plus population regulation at higher densities (candidate model 1), population regulation at higher densities with no Allee effects (candidate model 2) and no density dependence (candidate model 3). The Bayesian method used included a model selection procedure to identify which of the three forms of density dependence, represented in the candidate models, best fitted the data. I incorporated both process error (ω) and observation error. Observation error exists in both observed population densities and observed per capita growth rates. In chapter 3 I found that it was unnecessary to include observation error in observed densities in populations that only display high densities. This was because the observation error in observed growth rates associated with high densities is comparatively much larger than that of observed population densities. I also found that the density below which observation error in observed densities becomes important is 2.16. Observation error in the observed per capita growth rates and observed population densities was therefore only included when a population's minimum observed population density was less than 2.16, such that:

$$x_{t-1}{}^{true} \sim Gamma(x_{t-1}{}^{obs}, 1)$$

$$Y_t{}^{true} = f\left(X_{t-1}{}^{true}\right) + \omega$$

$$Y_t{}^{obs} \sim \mathcal{N}\left(Y_t{}^{true}, \sigma_t{}^2\right)$$

where,

$$Y_t = log\left(\frac{x_t}{x_{t-1}}\right) = X_t - X_{t-1};$$

$$\omega \sim \mathcal{N}(0, 1/\tau);$$

$$\tau \sim \text{Gamma}(10,1).$$

${x_t}^{obs}$and ${Y_t}^{obs}$ are observed population densities and logged observed per capita growth rate at time t, respectively, and ${x_t}^{true}$, ${X_t}^{true}$and ${Y_t}^{true}$ are true population densities, logged true population densities and logged true per capita growth rate at time t, respectively. ω is process error and was assigned an uninformative prior. An uninformative prior was used because it allows for a range of different process error estimates to be calculated which is necessary when applying the same method to a large number of different populations as each will be influenced by external factors to different extents. This was demonstrated in chapter 2 for external weather factors that varied quantitatively in their influence on population dynamics across 100 km square populations of the large skipper *Ochlodes sylvanus*. Standard deviation σ_t is calculated as shown in chapter 3, section 3.2.3. (pp. 41 and 42). $f\left({X_{t-1}}^{true}\right)$ is the density-dependent process part of the model. If a population's minimum observed population density was ≥ 2.16 only observation error in the observed per capita growth rates was included, such that:

$$ {Y_t}^{true} = f\left({X_{t-1}}^{obs}\right) + \omega $$

$$ {Y_t}^{obs} \sim \mathcal{N}\left({Y_t}^{true}, {\sigma_t}^2\right) $$

where ${X_t}^{obs}$ is logged observed population density.

$f\left({X_{t-1}}^{true}\right)$ took a different form of density dependence in each of the three candidate models that were tested in the model selection procedure. Candidate model 1 had negative quadratic density dependence which represents an Allee effect plus population regulation at higher densities, candidate 2 had negative linear density dependence which represents population regulation at higher densities with no Allee

effects and candidate 3 included only an intercept which represented no density dependence:

Candidate Model 1 $f\left({X_{t-1}}^{true}\right) = -\alpha_0 \left({X_{t-1}}^{true}\right)^2 + \alpha_1 {X_{t-1}}^{true} + \alpha_2;\ \alpha_0 > 0$

Candidate Model 2 $f\left({X_{t-1}}^{true}\right) = -\alpha_1 {X_{t-1}}^{true} + \alpha_2;\ \alpha_1 > 0$

Candidate Model 3 $f\left({X_{t-1}}^{true}\right) = \alpha_2$

where α_0, α_1 and α_2 are parameters with priors of normal distribution except when they have a preceding minus sign, in which case the priors had gamma distributions to ensure $-\alpha$ remained negative.

Bayesian analyses were carried out to assess each of the three candidate models for each population using WinBUGS version 1.4.3 and R version 2.15.2 (Lunn *et al.*, 2000; R Development Core Team, 2010). In order to analyse the WinBUGS outputs in R I used the 'bugs' function in the "R2WinBUGS" R package (Gelman *et al.*, 2013). Each run consisted of 20,000 iterations and 3 chains. The first half of iterations was discarded and to eliminate autocorrelation among a parameter's estimates within a chain, iterations were thinned so that every 3rd iteration was kept. To check for parameter convergence I firstly converted the WinBUGS output into the correct format using 'convert.to.coda' function in the "adaptMCMC" R package (Scheidegger, 2012). Using the 'gelman.diag' function in the "coda" R package I obtained convergence scores in the form of multivariate potential scale reduction factor (mpsrf) values (Plummer *et al.*, 2012). The mpsrf is a measure of the variance between chains compared to the variance within chains. When these variances are similar, the chains have reached their target distribution and therefore mpsrf scores less than 1.1 indicate chain convergence. In instances where the mpsrf score was above 1.1 I re-ran the analysis of the candidate

models with non-converged chains for 100,000, 200,000, 300,000 and 400,000 iterations, stopping when convergence was achieved.

For all converged candidate models the Deviance Information Criterion (DIC) was recorded. A model's DIC value is used as a measure of how well the model fits the data and can be compared between models for the same data. The model with the lowest DIC is the best model of the models being compared, although, when DIC values are similar this reflects that the suitability of the models is similar. In this study if, for a given population, model suitability of the two candidate models with the lowest DIC is similar, this suggests that the population experiences an alternative form of density dependence than is represented by those two candidate models. The candidate model with the third lowest DIC is less suitable than the other two candidate models and so is not an adequate model either. These populations with an indistinguishable form of density dependence through the model selection procedure used in this study were excluded from the second part of the analysis for which susceptibility to Allee effects is investigated. I categorised populations as having indistinguishable density dependence if the lowest DIC value was less than 0.1 smaller than the second lowest DIC value. I decided to use a relatively small criterion of 0.1 because of the small difference between DIC values of correct and incorrect models produced for the simulated data in chapter 3.

For populations with candidate model 1 selected as the best model, negative quadratic density dependence was the most suitable form of density dependence from the three forms tested. Negative quadratic density dependence can be indicative of an Allee effect, although if the observed data does not show reduced per capita growth rates at its lowest densities there is no evidence for an Allee effect being present, as illustrated for a hypothetical population in Fig. 4.1. b). The lowest observed density in Fig. 4.1. b) has

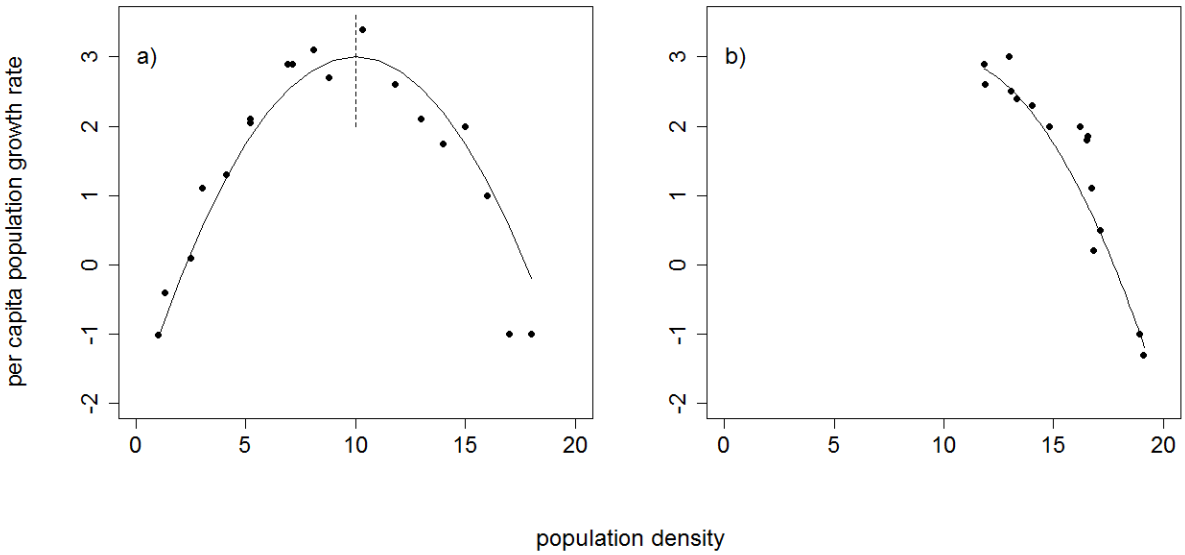

Fig. 4.1. Growth plots for two hypothetical populations that exhibit negative quadratic density dependence. Black dots represent hypothetical observed population densities and black lines shows the relationship between per capita growth rate and population density over the range of observed densities. a) illustrates a population that displays a reduction in per capita growth rate with a reduction in population density, at low densities. This indicates that the population undergoes an Allee effect. If the population does not display reduced per capita growth rate with reduced population density, as in plot b), an Allee effect cannot be detected. The dashed line in a) shows the density at which the turning point occurs. Only when observed densities are below the density associated with the turning point can an Allee effect be detected.

lower per capita growth rate than would be expected if the population was regulated by negative linear density dependence, and therefore the negative quadratic model is favoured by the model selection procedure. Fig. 4.1. a) shows a hypothetical population for which evidence of an Allee effect does exist, as a reduction in per capita growth rate occurs at the population's lowest densities. The reduction in per capita growth rate with decreased density results in the presence of a turning point (maximum), as indicated by the dashed line in Fig. 4.1. a), with densities that correspond to a reduction in per capita growth rate occurring below the density of the maximum. Butterfly populations that had negative quadratic density dependence selected as the most suitable form of density dependence (of the three tested) were categorised as Allee populations if their lowest observed density was below the population density at which the maximum occurs. This population density corresponding to the maximum was easily calculated from the parameter estimates of the negative quadratic equation. The maximum occurs when the differential of the negative quadratic equation equals zero:

$$y = -\alpha_0 {X_{t-1}}^2 + \alpha_1 X_{t-1} + \alpha_2$$

$$\frac{dy}{dX_{t-1}} = -2\alpha_0 X_{t-1} + \alpha_1 = 0$$

and so the maximum occurs at:

$$X_{t-1} = \frac{\alpha_1}{-2\alpha_0}$$

An Allee effect is a phenomenon that only occurs at low densities. Therefore, to assess a species' susceptibility to Allee effects it is necessary to consider the species' populations that exhibit low densities (populations with only high densities recorded may still be subject to Allee effects even though an Allee effect is not detected). To test

whether the detection of Allee effects depended on the minimum observed population density I ran binomial regressions for each species with presence or absence of Allee effect as the response variable and minimum observed population density as the explanatory variable. I did this separately for each species because the densities over which Allee effects occur could vary greatly between species. Had I carried out the regression indiscriminate of species this may have resulted in no relationship between the detection of Allee effects and population minimum density being found, and within species variation being unaccounted for. For species where presence of Allee effects were significantly influenced by minimum population density, populations displaying high densities only were eliminated before calculating the species' susceptibility to Allee effects. A population was defined as 'high densities only' if it had a larger minimum population density than the highest minimum population density of all Allee populations for the given species. This definition was based on the premise that if a population had a lower minimum density than another population of the same species for which an Allee effect was detected, then detection of an Allee in that population should have been possible. While identification of 'high densities only' populations was possible for species that had Allee populations, it was not possible for species that had no populations with detected Allee effects. Species that had no populations with detected Allee effects were therefore omitted from the susceptibility analysis because lack of detection of Allee effects did not necessarily indicate a species was not susceptible and could have been simply due to no populations with low enough densities being present in the data.

To check that the resulting proportion of populations exhibiting Allee effects per species did not depend on the total number of populations analysed per species, I ran a linear regression using the 'lm' function in the R package "stats".

4.2.2 Species Susceptibility to Allee Effects and Traits Analysis

I used the proportion of populations that showed evidence of Allee effects as a measure of each species' susceptibility to Allee effects, and investigated the influence of certain species' traits on this susceptibility to Allee effects. I tested for phylogenetic autocorrelation and subsequently accounted for it when testing the various species traits. I did this using Markov chain Monte Carlo Sampler for Generalised Linear Mixed Models (MCMCglmm), a function specifically designed to account for correlated random effects arising from phylogenies (Hadfield 2012). This function was accessed through the R package "MCMCglmm". Each individual test (one for phylogenetic autocorrelation and one for each species trait; six in total) consisted of 1000 MCMCglmm regressions, one regression for each of the 1000 phylogenetic trees I used. These phylogenetic trees represent different possible sets of phylogenetic relatedness across all commonly occurring British butterflies and were constructed by Oliver *et al.* (2012). These authors used Geneious (created by Biomatters) to search for genetic information for each species followed by tree constructions in Beast v1.5.4 (Drummond & Rambaut 2007) using the approach outlined in Drummond *et al.* (2006). Genetic information for *Erynnis tages, Hesperia comma* and *O. sylvanus* was not available and genetic information for congeners *E. tristis, H. florinda* and *O. ochracea* was used instead. The R package "ape" (Paradis 2013) was used in this study to read in phylogenetic trees and restrict them to include only the species analysed here. Four examples of the phylogentetic trees used are shown in Fig. 4.2, 4.3, 4.4 and 4.5. For each of the 1000 trees, I ran the MCMCglmm with susceptibility to Allee effects as a binomial response variable, a trait as the fixed-effect variable and phylogeny as random effects. The logit link function was applied when the MCMCglmm regression was carried out due to the response variable being binomial (in

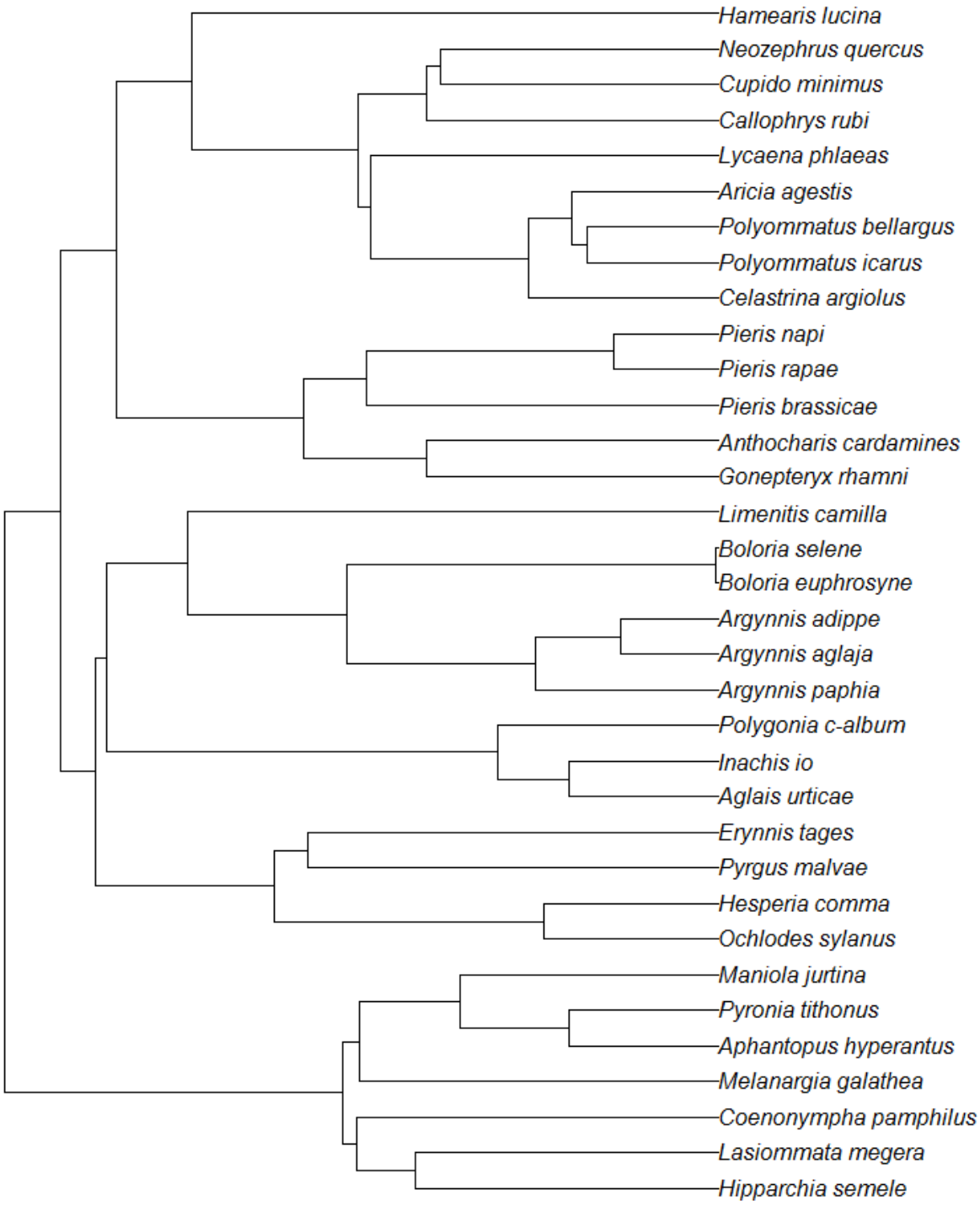

Fig. 4.2. First example phylogenetic tree after being restricted to the species included in this study's analysis of susceptibility to Allee effects. Original trees were obtained from the 1000 trees constructed by Oliver *et al.* (2012).

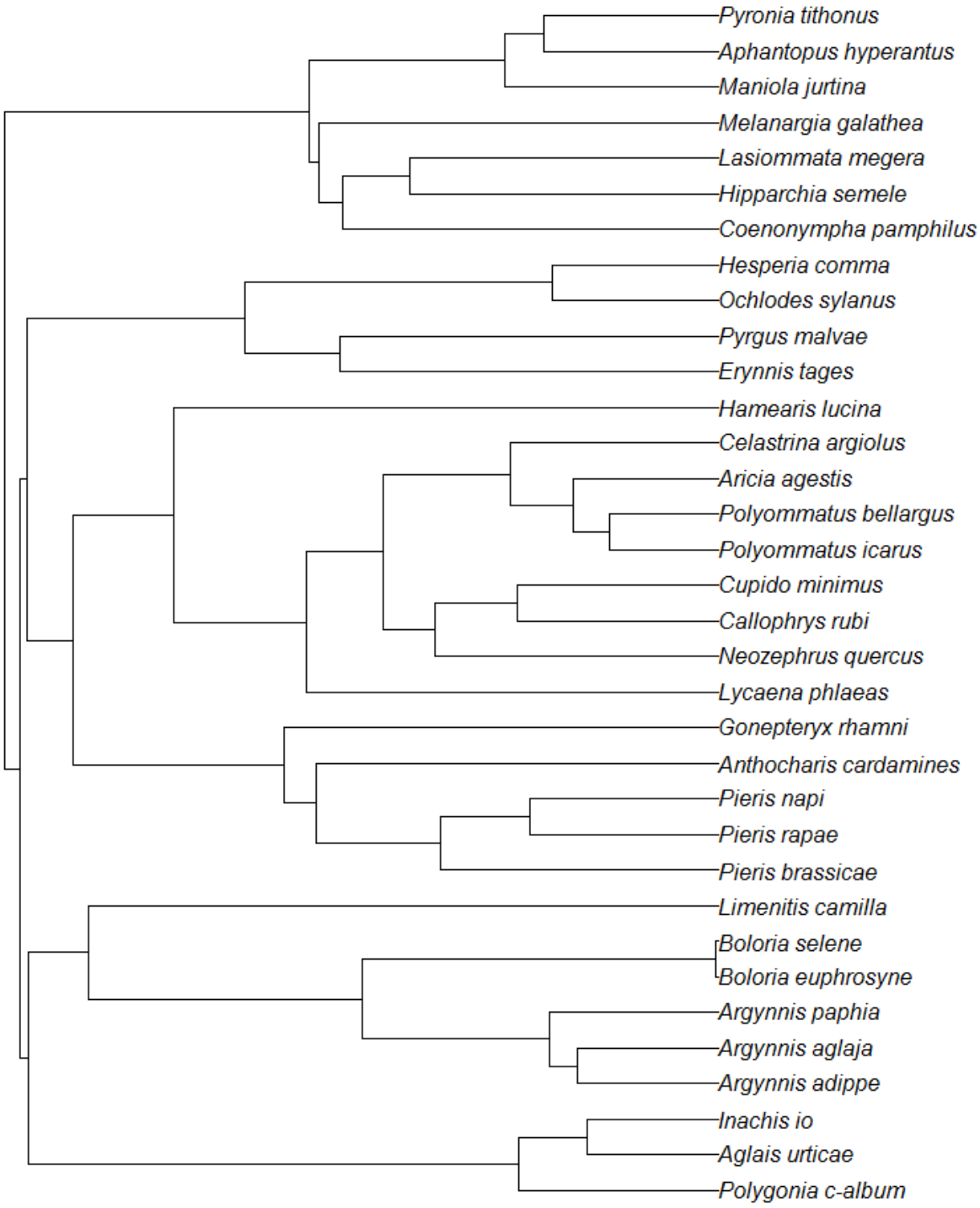

Fig. 4.3. Second example phylogenetic tree after being restricted to the species included in this study's analysis of susceptibility to Allee effects. Original trees were obtained from the 1000 trees constructed by Oliver *et al.* (2012).

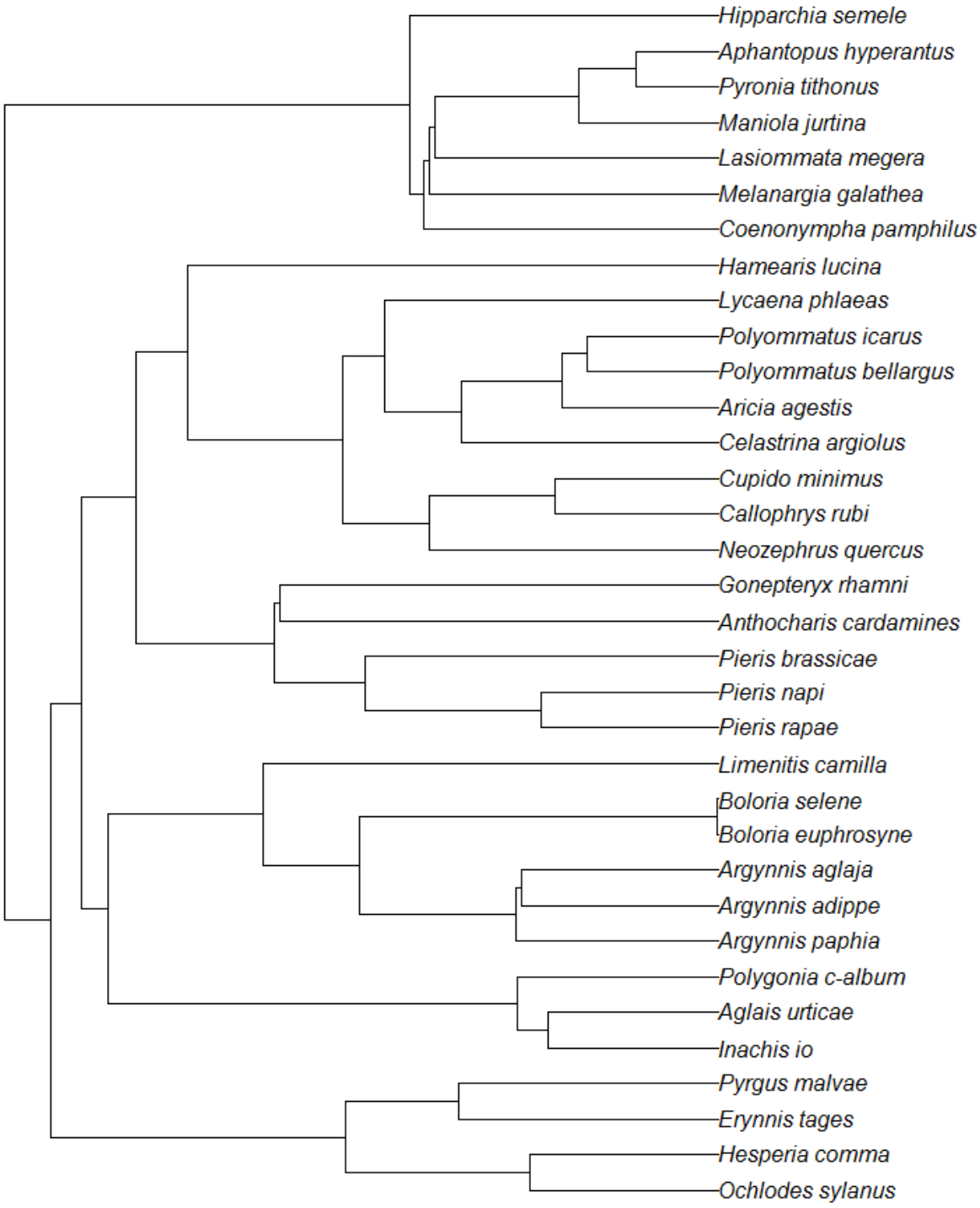

Fig. 4.4. Third example phylogenetic tree after being restricted to the species included in this study's analysis of susceptibility to Allee effects. Original trees were obtained from the 1000 trees constructed by Oliver *et al.* (2012).

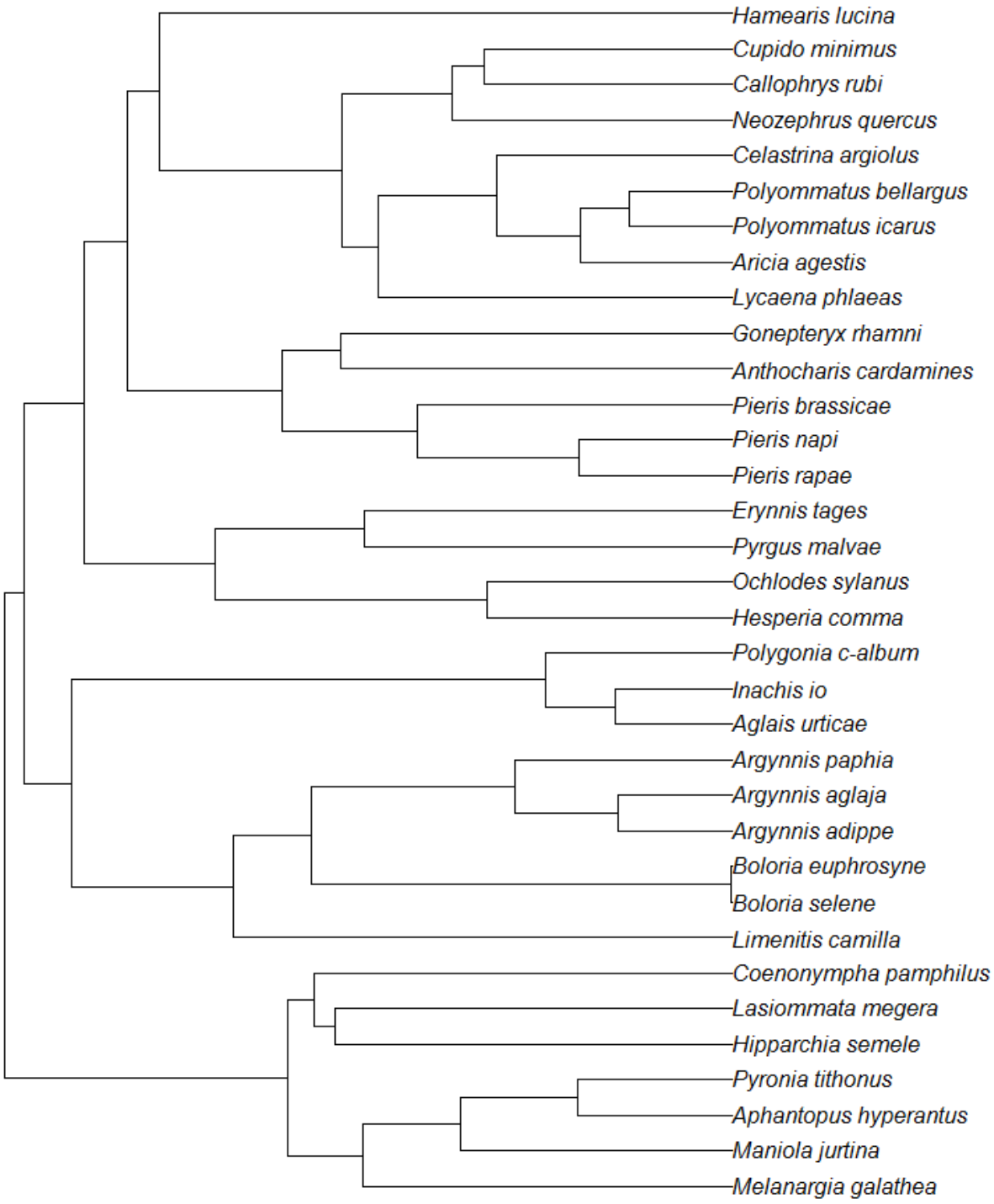

Fig. 4.5. Fourth example phylogenetic tree after being restricted to the species included in this study's analysis of susceptibility to Allee effects. Original trees were obtained from the 1000 trees constructed by Oliver *et al.* (2012).

the form of ‘number of Allee populations’ and ‘number of non-Allee populations’). Because MCMCglmm utilises Markov chains to produce probability densities for each parameter, parameter priors were needed. All priors in each susceptibility analysis were set to be uninformative as there are no previous studies that suggest how phylogeny will affect susceptibility to Allee effects. No fixed-effects were included in the null model used to test for phylogenetic autocorrelation. In each trait analysis, I collated the 1000 posterior densities for each model parameter and obtained the mode and Highest Posterior Density (HPD) intervals for each. The HDP intervals are the upper and lower values between which the probability content is 0.95. To accomplish this I used the HPDintervals function in the R package “coda” (Plummer *et al.* 2012).

The species traits tested consisted of three mate location sites (physical edge, host plant, nectar plant), the mate location method perching and mobility. Binary data were used for each of the three mate location sites and perching, for each species (Dennis 2010). Mobility scores varied from 1 to 9 with 1 for species with the least movement and 9 for species with the most movement (Dennis 2010). Scores were derived using the following 9 variables: ex-habitat vagrants, garden records, urban central business district records, at-sea records, mass movements, range expansions, overseas migration from continent to Europe, regular reversed long distance migration, over-ocean (Atlantic) migration (Dennis 1993; Dennis 2005).

In order to clearly illustrate the relationships between susceptibility to Allee effects and species traits I obtained the posterior density of the response variable, susceptibility to Allee effects, for a given value of a fixed-effect and the corresponding modal intercept. To do this I first needed to convert the MCMCglmm outputs as the logit link function was used as part of the analysis. The logit link function is:

$$logit(y) = \log\left(\frac{number\ of\ Allee\ populations}{total\ number\ of\ populations - number\ of\ Allee\ populations}\right)$$

where y is susceptibility to Allee effects, for a given species. After accounting for phylogeny the regression is carried out using:

$$logit(y) = \beta_0 + \beta_1 x$$

where β_0 is the posterior density of the intercept and β_1 is the posterior density of the slope of the fixed-effect x. To obtain the posterior density of the response variable I therefore used the following:

$$y = \frac{e^{(\beta_0 + \beta_1 x)}}{1 + e^{(\beta_0 + \beta_1 x)}}.$$

To illustrate the influence of a fixed effect I obtained a single posterior density of the response variable using only the mode of the posterior density of the intercept β_0, rather than calculating each posterior density of the response variable for each value in the intercept's posterior density. I could have set β_0 to be another single value and the same relationship would be illustrated, but I chose the mode of the intercept as a measure of central tendency from the posterior density. I plotted the resulting density of the response variable for set values of x to graphically display the supporting evidence for an increase or decrease in susceptibility to Allee effects due to each species trait (fixed-effect); for all binary species traits x was set to 1 and for mobility I obtained response variable posterior densities for two example x values, 3 and 8, in order to illustrate the

influence of mobility effectively. If both HDPintervals of the response variable posterior density lie above the mode intercept this is evidence of an increase in susceptibility to Allee effects with increased species trait, and if the HDPintervals of the response variable posterior density lie below the mode intercept this is evidence of a decrease in susceptibility to Allee effects with increased species trait. For binary species traits 'increased species trait' signifies adoption of that trait, e.g. adopting perching behaviour or adopting physical edges as mating location sites. For mobility 'increased species trait' simply signifies an increase in mobility score.

4.3 Results

4.3.1 Bayesian Analysis

A total of 38 species met the minimum criteria required to be included in this study. Across the 38 species a total of 5934 individual populations that differed in both species and site were analysed. Of these I obtained a best model for 4744 populations, the other 1190 populations had their two best models differing in DIC value by less than 0.1 and were therefore eliminated from the susceptibility to Allee effects analysis. Of the 4744 populations, 906 populations (19% of the total populations) exhibited negative quadratic density dependence, 2598 populations (55% of the total populations) showed negative linear density dependence and for 1240 populations (26% of the total populations) the null model was found to be the best of the three candidate models. Of the 906 populations displaying negative quadratic density dependence 340 had observed densities below a population's turning point (maximum) and were therefore categorised as Allee populations. The other 566 population with negative quadratic density dependence did not show evidence of Allee effects.

A decrease in minimum population density caused an increase in the detection of an Allee effect for four species *Limenitis camilla, Pararge aegeria, Pieris brassisae* and *Pieris napi* (Fig. 4.6. a-d; see Appendix C, Table C.1. for all species results). After eliminating 'high densities only' populations the detection of Allee effects in *L. camilla, P. brassisae* and *P. napi* were no longer significantly affected by minimum population density (Fig. 4.6. e, g, h; Appendix C, Table C.2.) and the proportion of populations that showed evidence of Allee effects for these three species was calculated after elimination of the 'high densities only' populations. However, detection of Allee effects was still negatively influenced by minimum population density for *P. aegeria* (Fig. 4.6. f; Appendix C, Table C.2.). This was due to one of the *P. aegeria* Allee population's having a relatively high minimum population density and so many populations not exhibiting Allee effects remained in the analysis after population elimination was carried out. From these results it is unclear which *P. aegeria* populations have low enough densities to allow Allee effects to be detectable. For this reason I omitted *P. aegeria* from the remainder of the analysis.

The mean proportion of populations showing evidence of Allee effects, per species, was 0.08. Three species showed no evidence of Allee effects across their populations. These species were *Euphydryas aurinia, Leptidea sinapis* and *Polymmatus coridon.* The species with the highest proportion of populations showing evidence of Allee effects were *Pyrgus malvae* and *Argynnis adippe*, both with a proportion of 0.18. Fig. 4.7. shows a histogram of proportion of species populations with Allee effects. The proportion of populations showing evidence of Allee effects, per species, did not depend on the total number of populations, per species ($t=-1.31$, $df=35$, $p=0.199$).

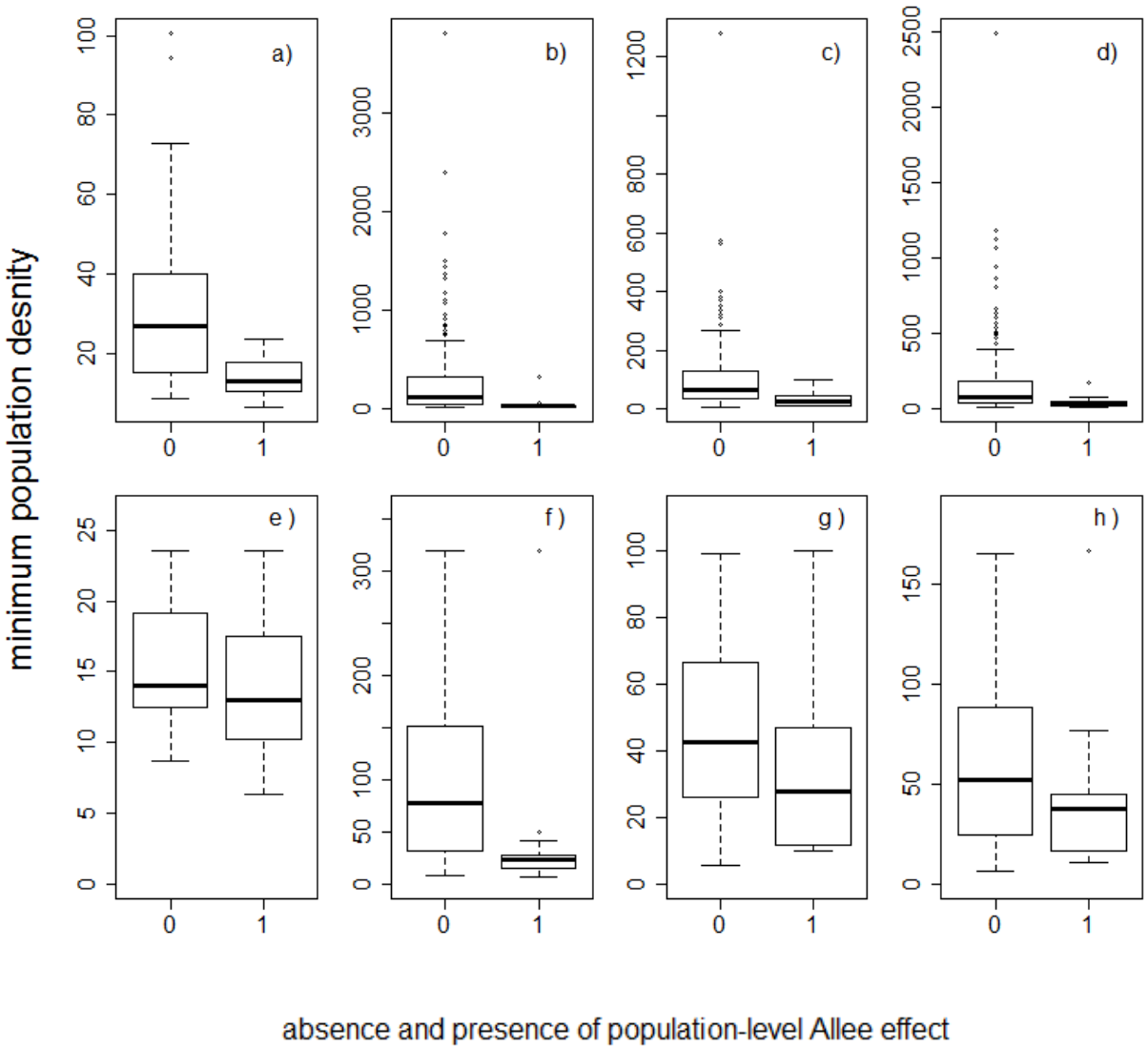

Fig. 4.6. Boxplots of minimum population density for populations with (1) and without (0) Allee effects for *Limenitis Camilla* (a, e), *Pararge aegeria* (b, f), *Pieris brassisae* (c, g) and *Pieris napi* (d, h). Presence of an Allee effect was significantly (and negatively) affected by minimum population density for these four species when all populations that were categorised by their density dependence via the model selection process were considered – this relationship is illustrated for the four species in a-d. After elimination of 'high-densities only' populations (see chapter 4, section 4.2.1., pp. 68 for selection criteria of this elimination) presence of an Allee effect was not significantly affected by minimum population density for *L. camilla* (e), *P. brassisae* (g) and *P. napi* (h), but was still significantly affected by minimum population density for *P. aegeria* (f).

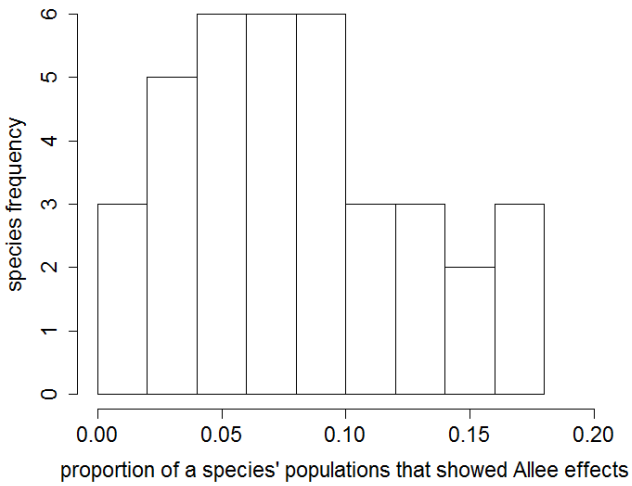

Fig. 4.7. Histogram for the proportion of a species' populations that showed Allee effect. Total number of species is 37 (*Pararge aegeria* is not included here as an accurate proportion of populations showing Allee effects could not be deduced). Three species *Euphydryas aurinia, Leptidea sinapis* and *Polymmatus coridon* had no populations displaying Allee effects.

4.3.2 Species Susceptibility to Allee Effects and Traits Analysis

The three species for which no populations exhibited Allee effects (*E. aurinia, L. sinapis* and *P.coridon*) were omitted from the susceptibility to Allee effects analysis. Susceptibility to Allee effects was defined as the proportion of a species' populations that showed evidence of Allee effects, and will be referred to as susceptibility to Allee effects throughout the remainder of this results section.

Phylogeny influenced species' susceptibility to Allee effects. The linear regression (using MCMCglmm) of the null model with phylogeny as random effects resulted in the posterior density of phylogeny having a mode of 0.54, and upper and lower HPDintervals of 0.25 and 0.82, respectively. The non-overlap of zero indicates a significant influence of phylogeny on susceptibility to Allee effects. As phylogeny influenced susceptibility to Allee effects, phylogeny was accounted for in the subsequent species traits analyses. Fig. 4.8. shows the posterior densities for heritability (phylogeny), and intercept and slope of the fixed effect species trait, with each row displaying posterior densities for each species trait analysis (five in total). The dashed lines show the HDPintervals of each posterior density and indicate the upper and lower boundaries between which the probability content is 0.95. The estimates of the posterior densities are a result of using the logit link function during analyses. Transformation of results showed the mode intercept to be 0.113 for host plant mating location sites, i.e. for species that do not use host plant mating location sites the mode susceptibility to Allee effects is 0.113. The mode susceptibility to Allee effects was 0.066, 0.094 and 0.087 for species that do not use physical edge mating location sites, for species that do not use nectar mating location sites and for species that do not use perching behaviours, respectively. The mode intercept for mobility was 0.113 which reflects the susceptibility to Allee effects of a

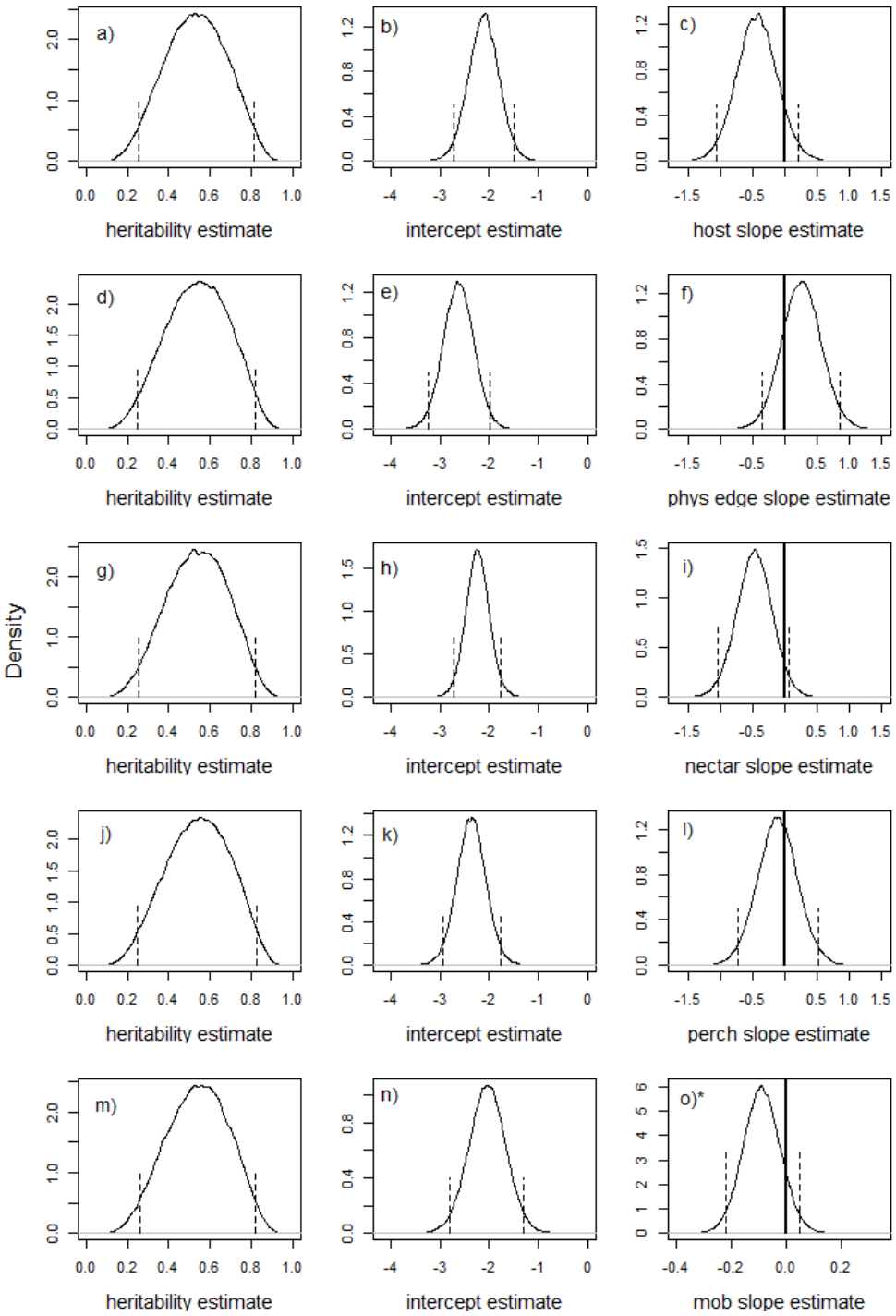

Fig. 4.8. Posterior densities for heritability (phylogeny), intercept and slope of the fixed effect species trait, with each row displaying posterior densities for each species trait analysis (host plant mating location site (a-c); physical edge mating location site (d-f); nectar plant mating location site (g-i); perching mate-locating behaviour (j-l); mobility (m-o)). The dashed lines show the HDPintervals of each posterior density and indicate the upper and lower boundaries between which the probability content is 0.95. The thick vertical line in plots c, f, i, l and o show where in the posterior density the estimate equals 0. For all fixed-effect slopes 0 is within the HDPintervals, therefore none of the five fixed-effects are significant. The estimates are of untransformed MCMMglmm outputs (for transformed results see text and Fig. 4.9 and 4.10.)

***different x-axis scale used.**

hypothetical species of zero mobility. Fig. 4.8. c, f, i, l and o show the posterior densities for the species trait in each of the five analyses. In each of these trait posterior densities, zero is found between the HDPintervals indicating that none of the traits examined significantly influenced susceptibility to Allee effects. However, a negative trend in susceptibility to Allee effects with the use of nectar mating location sites was apparent as the upper HDPinterval was very close to zero (Fig. 4.8. i). Similarly, a negative trend between mobility and susceptibility to Allee effects is shown in these results (note the different x-axis scale used for mobility in Fig.4.8. o). While use of nectar mating location sites and mobility were not significant effects these identified trends indicate that further examination is required before their influence on susceptibility to Allee effects can be fully understood.

Fig. 4.9. a, c, e and 4.10. a, c show how susceptibility to Allee effects varied for each species trait. Fig. 4.9. and 4.10. show resultant susceptibility to Allee effects densities for species that use host plant mating location sites (4.9. b), for species that use physical edge mating location sites (4.9. d), for species that use nectar plant mating location sites (4.9. f) and for species that use perching behaviour to locate mates (4.10. b). The thick black horizontal line indicates the mode intercept, i.e. the mode value for species that do not adopt the given species trait. Fig. 4.10. d) shows the resultant susceptibility to Allee effects densities for species with mobility of 3 (black curve) and 8 (red curve). The dashed lines for all density plots in Fig. 4.9 and 4.10 indicate the HDPintervals. Fig. 4.9 f) and 4.10 d) illustrate again the negative trends associated with the use of host plant mating location sites and increased mobility, respectively, have on susceptibility to Allee effects.

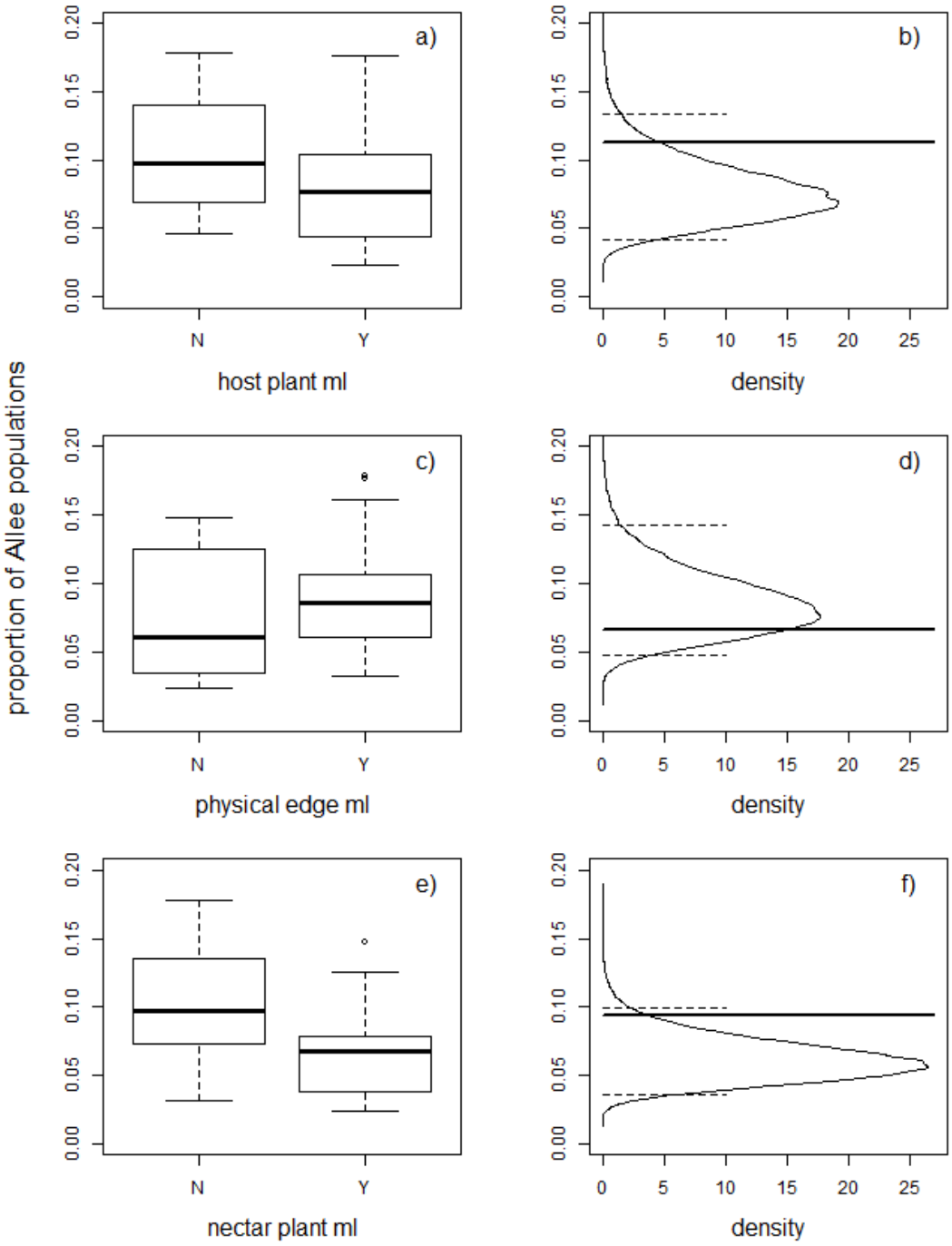

Fig. 4.9. Plots of the relationship between a species' proportion of Allee populations and species trait, where species trait is host plant mating location site in a), physical edge mating location site in c) and nectar plant mating location site in e). Y indicates species that do utilise the mating location site and N indicates species that do not utilise the mating location site. These relationships have not been adjusted to account for phylogenetic relatedness. Plots b, d and f) show the posterior densities of proportion of Allee populations for species that utilise host plant mating location sites (b), physical edge mating location sites (d) and nectar plant mating location sites (f) calculated using the transformed mode of the intercept's posterior density (Fig. 4.8. b, e and h, respectively) and slope posterior densities (Fig. 4.8. c, f and i, respectively) results from the traits analyses. The dashed lines in b, d and f) show the HDPintervals for the corresponding posterior density.

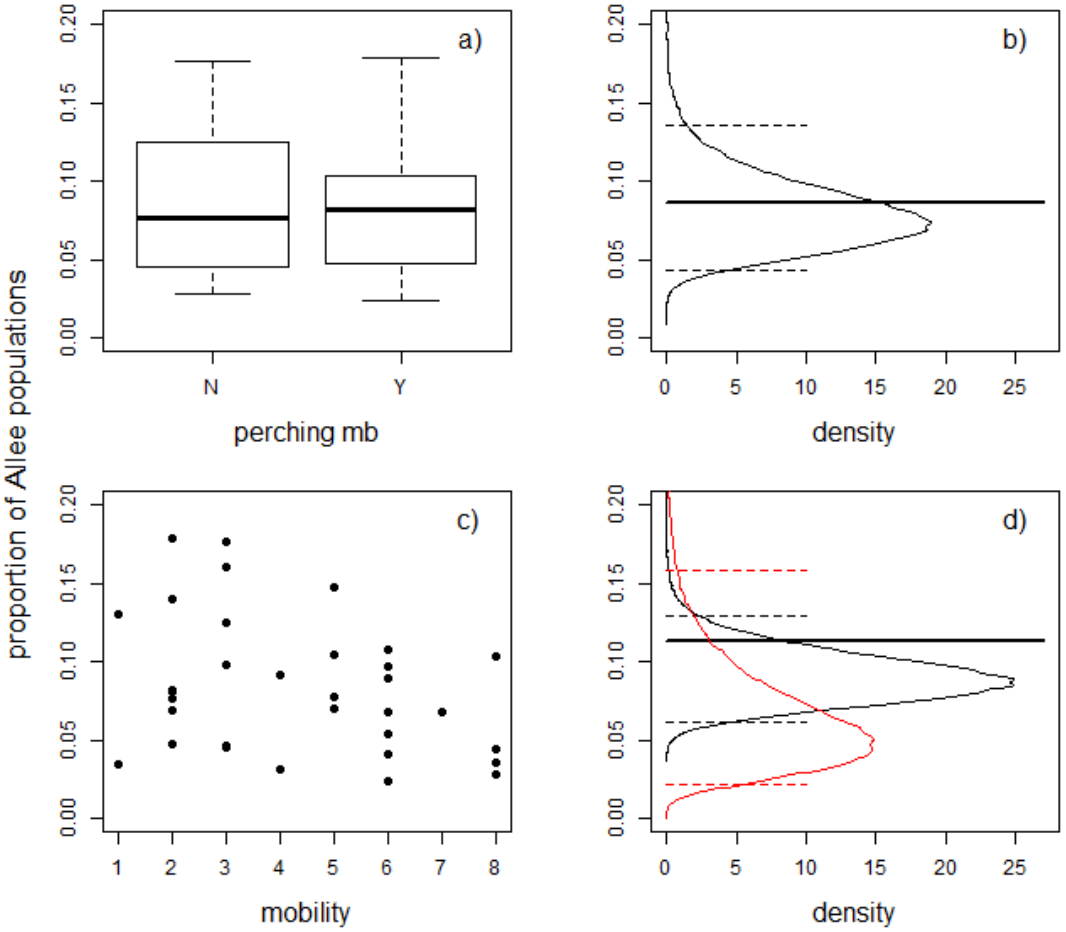

Fig. 4.10. Plots of the relationship between a species' proportion of Allee populations and species trait, where species trait is perching mate-locating behaviour in a) and mobility in c). Y indicates species that do utilise the perching mate-location behaviour and N indicates species that do not. These relationships have not been adjusted to account for phylogenetic relatedness. Plots b and d) show the posterior densities of proportion of Allee populations for species that utilise perching mate-location behaviour (b), have a mobility score of 3 (d, black curved line) and have a mobility score of 8 (d, red line). These were calculated using the transformed mode of the intercept's posterior density (Fig. 4.8. k, n and n, respectively) and slope posterior densities (Fig. 4.8. l, o and o, respectively) results from the traits analyses. The dashed lines in b and d show the HDPintervals for the corresponding posterior density (colour coded in d).

The three species included in this analysis known to utilise lekking mating systems had 9% (*Coenonympha pamphilus*), 7% (*Ochlodes sylvanus*) and 16% (*Neozephyrus quercus*) of their populations exhibiting Allee effects.

Spatial distribution of Allee and non-Allee populations are shown for species with the lowest susceptibility to Allee effects (*Maniola jurtina*, Fig. 4.11), median susceptibility to Allee effects (*Melanargia galathea*, Fig. 4.12) and highest susceptibility to Allee effects (*Pyrgus* malvae, Fig. 4.13).

4.4 Discussion

Thirty-five British butterfly species showed evidence of population-level Allee effects while three species exhibited no Allee effects. Species' susceptibility to Allee effects was investigated across all species showing evidence of Allee effects, with the exception of *Pararge aegeria*, which was excluded from the interspecies analysis as its susceptibility to Allee effects could not be measured accurately. Detection of Allee effects was made possible by a model selection procedure of models containing different forms of density dependence, all of which incorporated both process error and observation error. The detection of an Allee effect was only influenced by minimum population density for four species. This is surprising because Allee effects can only be detected at low densities and their prevalence throughout populations with varying minimum population density for any given species was not expected. Carrying capacity has been shown to vary between habitat patches depending on resource availability within each habitat (Belovsky & Slade 1995), and it is possible that the population densities over which Allee effects may occur also vary with habitat quality or type. Possible mechanisms driving this spatial variation may include variation in movement facilitation due to differing habitat types or

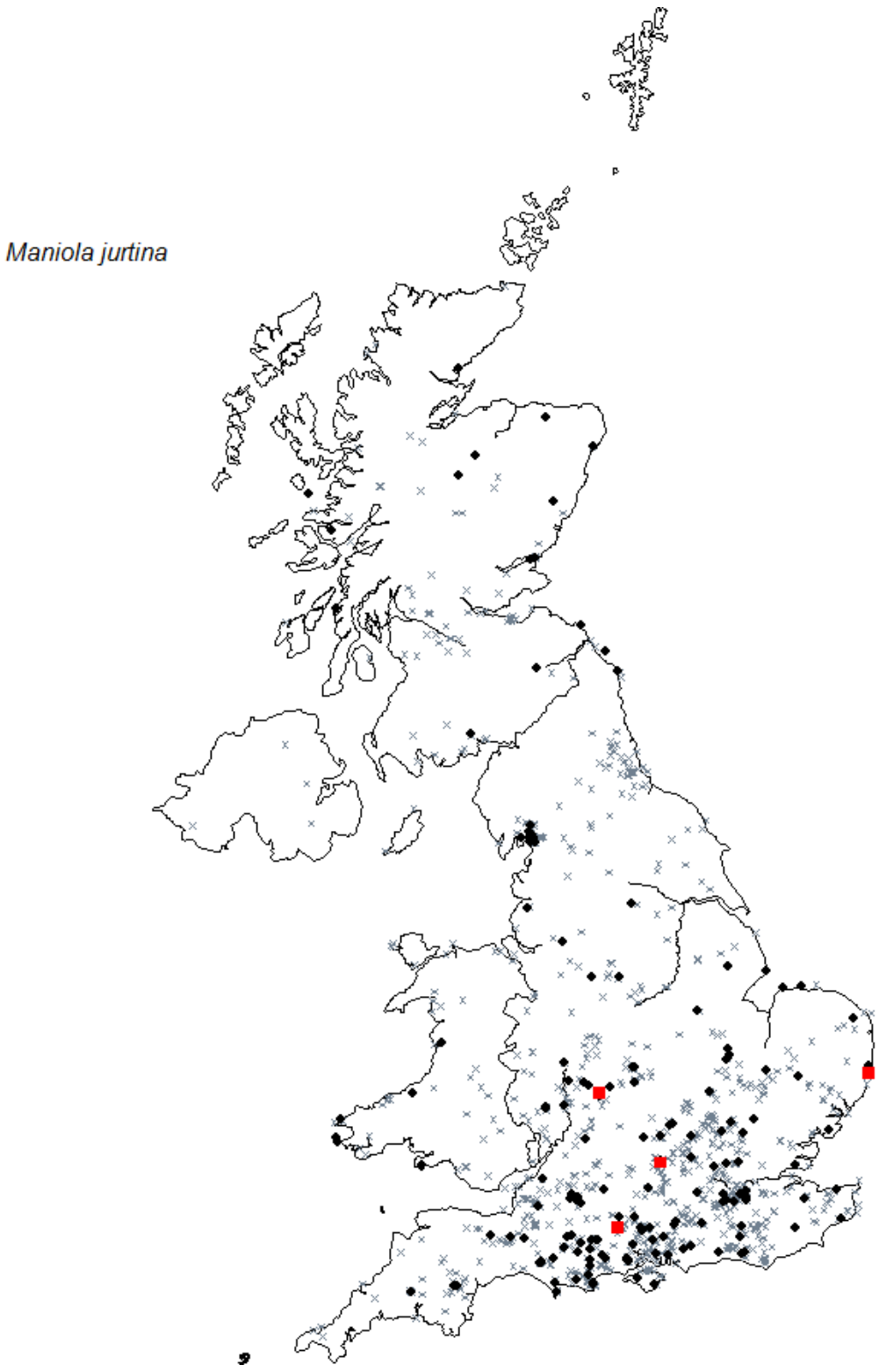

Fig. 4.11. Distribution of *Maniola jurtina* populations with differing forms of density dependence. Red squares show populations exhibiting Allee effects. Black diamonds show populations that had no density dependence, negative linear density dependence or negative quadratic density dependence at high densities. Grey crosses show populations for which the form of density dependence was not distinguishable or insufficient data was available for the analysis to be carried out. This species had the lowest susceptibility to Allee effects of the 34 species included in the susceptibility to Allee effects analysis.

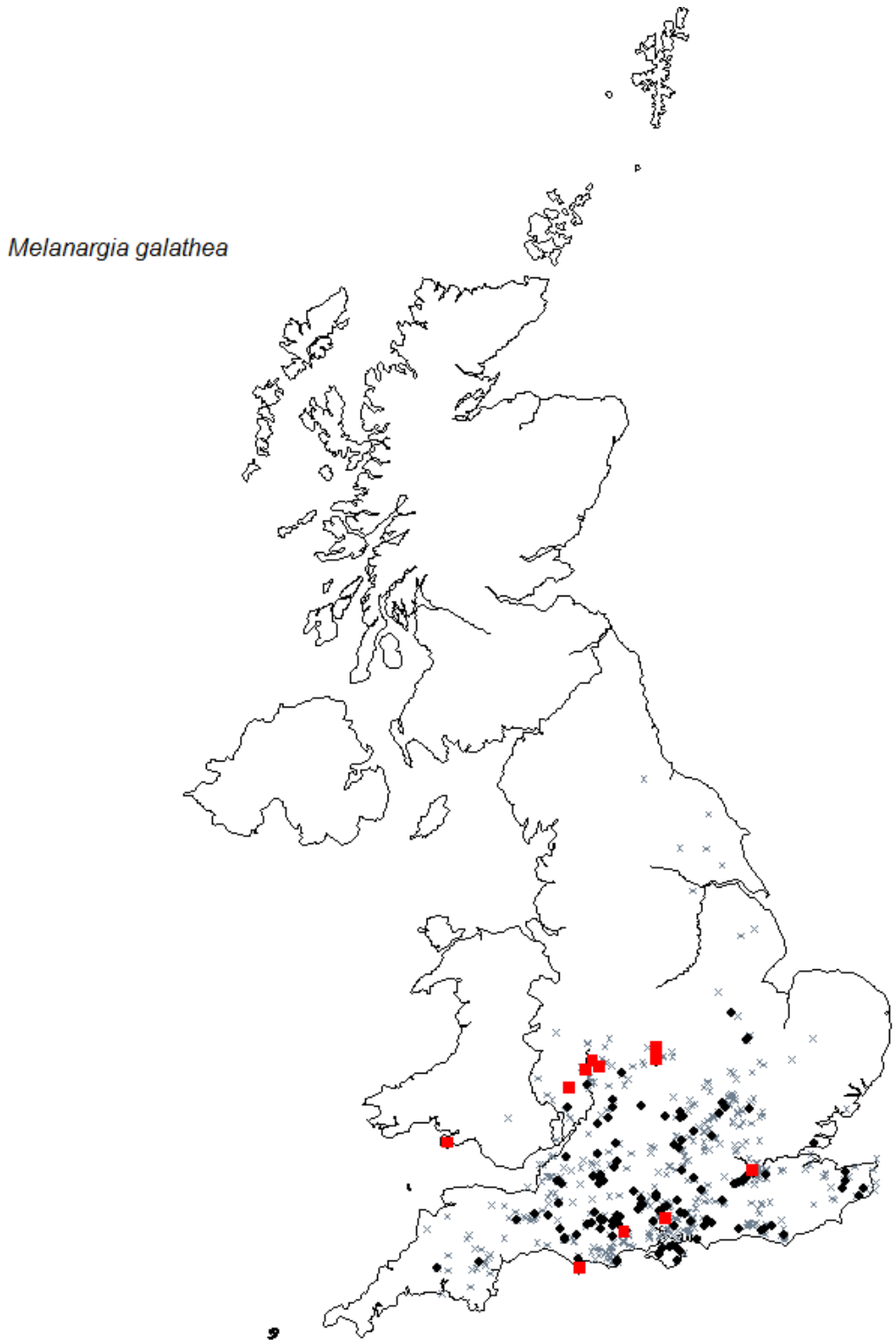

Fig. 4.12. Distribution of *Melanargia galathea* populations with differing forms of density dependence. Red squares show populations exhibiting Allee effects. Black diamonds show populations that had no density dependence, negative linear density dependence or negative quadratic density dependence at high densities. Grey crosses show populations for which the form of density dependence was not distinguishable or insufficient data was available for the analysis to be carried out. This species had the median susceptibility to Allee effects of the 34 species included in the susceptibility to Allee effects analysis.

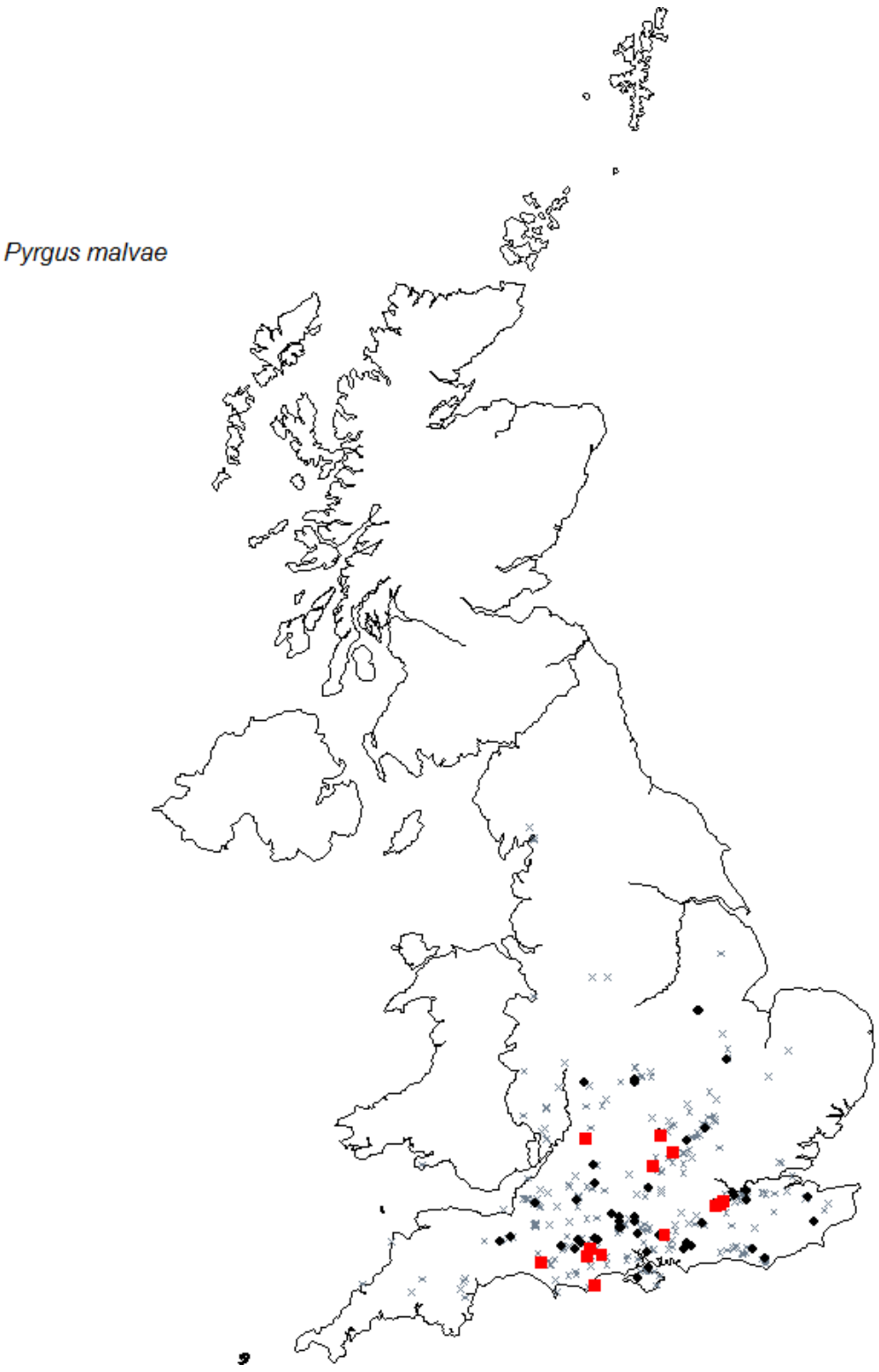

Fig. 4.13. Distribution of *Pyrgus malvae* populations with differing forms of density dependence. Red squares show populations exhibiting Allee effects. Black diamonds show populations that had no density dependence, negative linear density dependence or negative quadratic density dependence at high densities. Grey crosses show populations for which the form of density dependence was not distinguishable or insufficient data was available for the analysis to be carried out. This species had the highest susceptibility to Allee effects of the 34 species included in the susceptibility to Allee effects analysis.

structures, and variation in the provision of locations at which aggregations occur due to differences in habitat quality.

In addition to spatial variation in Allee thresholds there may also be temporal variation. Again, this has been shown for the carrying capacity which can vary temporally due to fluctuations in weather or habitat management (Belovsky & Slade 1995). This variation is caused by external factors influencing resource availability which in turn sets a population's carrying capacity (Sinclair 1989). Temporal variation in a population's Allee threshold and carrying capacity may have contributed to a large number of butterfly populations showing neither of the two forms of density dependence tested in the model selection procedure. While sensitivity of butterflies to direct weather effects is well known (Dennis 1993), little work has been carried out on the indirect influences of weather. Further understanding of these influences would allow us to estimate the variation in density-dependent related equilibria and help us understand the impact this has on detecting density dependence. The null model may also have been selected for such a large number of populations due to the restricted forms of density dependence tested for in this analysis. Testing alternate relationships between per capita growth rate and population density would provide more information about possible density dependence in these populations for which the null model was selected.

For 20% of populations a best model could not be distinguished. This could be due to the impact of observation error on ecological empirical analyses. Observation error in data obscures the true ecological processes and, even when accounted for, it may still lead to a number of possible outcomes given the data, in this case different forms of density dependence.

Susceptibility to Allee effects was significantly affected by phylogeny, suggesting that closely related species may have evolved similar adaptations and behaviours that govern the extent to which they are vulnerable to Allee effects. A number of studies have investigated the influence of phylogeny on species distribution and abundance (Lawton 1993, Gaston *et al.* 2000), but phylogenetic comparative analyses are rarely investigated for population dynamics (see Zanotto *et al.* 1996 for one example). To my knowledge this study is the first to unveil a link between phylogeny and Allee effects, and highlights the importance phylogeny has on population dynamics. Closely related Satyrinae species *Maniola jurtina, Pyronia tithonus* and *Aphantopus hyperantus* had similar and relatively low susceptibility to Allee effects, and closely related Nymphalidae species *Argynnis aglaja, Argynnis adippe, Argynnis paphia* and *Limenitis camilla* had similar and relatively high susceptibility to Allee effects. Identifying groups with similar susceptibility to Allee effects may allow predictions to be made about other species, for which too little data is available for density dependence analyses. This could be particularly important for endangered and rare species.

Species that utilise host plant sites for mating locations did not vary in susceptibility to Allee effects from species that do not utilise host plant sites for mating locations. Similarly, susceptibility to Allee effects did not vary between species that do and do not used physical edge sites as mating locations. Species that use nectar plant sites as mating locations showed lower susceptibility to Allee effects compared to species that did not use nectar plant sites as mating locations, however, this result was not quite significant. These results may be due to aggregations in specific mating location sites being influenced by how many other mating location sites a species utilises and how abundant these sites are throughout a habitat patch. To explore the role of mating

location sites in susceptibility to Allee effects further, a better understanding of aggregated mating systems across all British butterfly species needs to be achieved. In addition, information about how aggregated mating systems vary with habitat quality or type would indicate whether future work should focus on the influence of spatial variation across a species' populations on susceptibility to Allee effects. The three species known to form leks did not have comparatively low susceptibility to Allee effects as expected, suggesting that lekking behaviour does not reduce a species vulnerability to Allee effects.

Species that adopt perching mate-locating behaviour were not found to be more or less susceptible to Allee effects than patrolling-only species. This may be because species that only patrol in order to find mates may have evolved other traits to enhance their mate finding ability, assuming that the mechanism driving Allee effects is mate limitation, i.e. perching may be a poor indicator of mating success at low densities. Perching behaviour is also complicated by the fact that it varies with both weather and phenotype (Dennis & Williams 1987; Van Dyke *et al.* 1997).

I found that species mobility did not affect species' susceptibility to Allee effects. This suggests that mobility is far too simple a measure for exploring the influence of dispersal on a species' vulnerability to Allee effects. The ability of individuals to disperse between populations is largely influenced by how well the populations are connected, in addition to species mobility. However, evaluating a population's connectivity to other populations can be complex due to the heterogeneity of the interpatch matrix (Ricketts 2001). Also, incorporating the combined effect of connectivity and mobility may still not provide useful results as dispersal ability is complicated by the fact that dispersers can both immigrate as well as emigrate.

One notable feature of my results, however, is the spatial variation of Allee populations. For any given species, populations experiencing Allee effects do not appear to be clustered and instead seem to be spread out randomly across a species range (Fig. 4.11, 4.12 and 4.13). Cluster analyses may provide more information about spatial patterns of Allee populations.

Chapter 5: Consequences of localised Allee effects on network population synchrony

5.1. Introduction

Synchronisation between populations is a key aspect of spatiotemporal population dynamics (Lloyd and May, 1999; Liebhold, *et al.* 2004) and understanding its causes is paramount, as population synchrony can result in detrimental consequences such as disease outbreaks, pest outbreaks and elevated extinction risk (Liebhold *et al.,* 1996; Heino *et al.,* 1997; Grenfell *et al.,* 1998; Earn *et al.,* 2000; Grenfell *et al.,* 2001). Synchronisation may arise when populations are connected by dispersing individuals (Pecora & Carrol, 1990; Strogatz & Stewart, 1993; Goldwyn & Hastings, 2011), or by spatially correlated extrinsic factor, such as weather (known as the Moran effect, Moran, 1953). Although population synchrony has been studied extensively for a wide range of ecological systems (see Liebhold *et al.* 2004, pg 470, Table 1 for a comprehensive list), few have considered the influence of Allee effects. One case in which the link between Allee effects and population synchrony has been documented is the gypsy moth, an invasive species that has become a major pest to hardwood trees in eastern United States (Tobin *et al.* 2007; Bjornstad *et al.* 2010). While this case study shows significant evidence for Allee effects in gypsy moth invasions, to my knowledge no studies have investigated the relationship between strength of Allee effects and population synchrony, potentially a key factor to understanding the degree to which wild populations synchronise. In this chapter I examine this relationship, along with the influence of connectivity under different Allee

effect strength regimes, in a theoretical framework by measuring and comparing population synchronies of networks of varying localised Allee effects.

There are a number of ways in which population synchrony can be measured and Liebhold *et al.* (2004) provides a thorough review of the advantages and disadvantages of each. One of the two main methods involves calculating zero lag correlation scores and the other involves measuring phase coherency for pairs of time series. Zero lag cross-correlations can be made between time series of log-abundances or differences in log-abundances which considers perfect synchrony as populations increase and decrease together (Hanski & Woiwood 1993; Steen *et al.* 1996; Koenig 1999; Bjornstad *et al.*1999). Liebhold *et al.* (2004) highlights the issues of long term trends and temporal autocorrelation when using the zero lag cross-correlation approach, and discusses detrending and 'prewhitening' methods that have been developed to address such issues. Detrending removes long term trends, for example due to climate change, and allows any synchrony present between short-term fluctuations to be identified (Buonsccorsi *et al.* 2001). 'Prewhitening' removes serial dependence and has been used in a number of studies (Hanski & Woiwood 1993; Sutcliffe *et al.* 1996; Paradis *et al.* 1999; Powney *et al.* 2012). However, Buonsccorsi *et al.* 2001 raises concern about this form of time series manipulation, as it may result in existing population synchrony being discounted.

Synchronised populations cycle with the same frequency but may not necessarily reach the peaks and troughs of their cycles at the same time. For this reason population synchrony is analogous to phase locking, a phenomenon found in many complex systems ranging from an Asian fire fly population flashing in unison to electrons in a superconductor (Strogatz 2003). Phase locking refers to the cyclic behaviour of two coupled oscillators maintaining a constant phase difference over time, possibly after an

initial transient period directly following the coupling event. Therefore, zero lag cross-correlations methods may be sufficient when synchronised populations are at the same phase in their cycles at the same time, but may not be sufficient when cycling out of phase, as demonstrated by Liebhold *et al.* (2004). In light of this problem, measures of phase coherency that allow for lagged synchrony have been favoured (Blasius *et al.* 1999; Haydon & Greenwood 2000; Grenfell *et al.* 2001; Cazelles & Stone 2003). This method, however, relies on one's ability to identify population cycles which in some cases, e.g. in highly stochastic systems, may restrict its use. For the purpose of this theoretical study, where population cycles are easy to identify, I have utilised a measure of phase synchrony proposed by Cazelles & Stone (2003).

When dispersal between populations is so great the metapopulation concept breaks down as discrete breeding populations are less pronounced and population dynamics are largely governed by dispersal as opposed to localised ecological processes. In order to assess the influence of localised density-dependent processes it is necessary, therefore, to have low dispersal between populations. Networks with low levels of dispersal are 'weakly coupled'. I first investigated how population synchrony varied with network connectivity for given strengths of population level Allee effects in order to assess what level of connectivity reflects a weakly coupled network. I then examined how strength of population level Allee effects influence population synchrony in weakly coupled networks. Finally, I explored more realistic scenarios where populations differ in strength of Allee effects across a network.

5.2. Methods

5.2.1. Population Dynamics of Isolated Populations

As a precursor to assessing the impact of Allee effects on the dynamics of populations within connected networks I examined the dynamics of isolated populations. To achieve this I simulated time series using the following equation (Courchamp, Grenfell and Clutton-Brock (1999)):

$$\boldsymbol{x_t = x_{t-1}\left(\exp\left(\lambda\left(1-\frac{x_{t-1}}{K}\right)\left(1-\frac{A}{x_{t-1}}\right)\right)\right)} \qquad \text{(Eq. 5.1.)}$$

where x_t is population density, K is the population's carrying capacity, A is the Allee constant, λ is the maximum reproductive potential of an individual. Using Eq. 5.1. allowed the population dynamics to be governed by Allee effects in addition to being regulated around an equilibrium population density, to emulate resource limitation. The carrying capacity, K, was set to 30 for all populations generated.

Although synchrony is a widespread phenomena in weakly coupled systems, there is limited information about the influence of Allee effects on synchrony. I therefore wanted to create networks where either synchronisation or desynchronisation of localised population dynamics was a possible outcome once the network's populations were connected. I did this by generating populations with semi-chaotic dynamics when isolated, so that once connected localised dynamics could either become fully chaotic indicating desynchronisation or become cyclic in a system of increased synchrony. To obtain semi-chaotic dynamics for populations with varying strengths of Allee effects, I needed to select a suitable λ value. I first narrowed down the possible values of λ by

generating time series of 12,000 time steps for varying λ values with A set to 0. I discarded the initial 9,000 time steps so that transient dynamics were no longer occurring and assessed the population densities of the final 3,000 time steps by constructing a bifurcation plot. I repeated this process for varying A and set λ values, and selected the λ that allowed semi-chaotic dynamics to occur for the range of A values tested.

5.2.2. Network Population Dynamics

I created networks with a simple regular structure to emulate a metapopulation of 20 populations each connected to their nearest neighbours (Fig. 5.1. a). Individual population underwent migration and then localised density dependence as described above (Eq. 5.1.), in each time step. The strength of migration depended on the population density of the population from which dispersers emigrated, but did not depend on the population density of the population which dispersers immigrated to. Because of this it was necessary to apply the migration event and Eq. 5.1. sequentially, so that individuals that had emigrated from a population weren't falsely contributing to that population's density-dependent growth and, similarly, immigrating individuals were not falsely excluded from contributing to that population's density-dependent growth. Migration and density-dependent processes could equally have been carried out in the opposite order which would have possibly yielded different population densities (as I would have been measuring densities at a different point within the two step cycle) but the overall series of ecological process would be exactly the same across all time, and therefore the resulting patterns of population dynamics would have been the same.

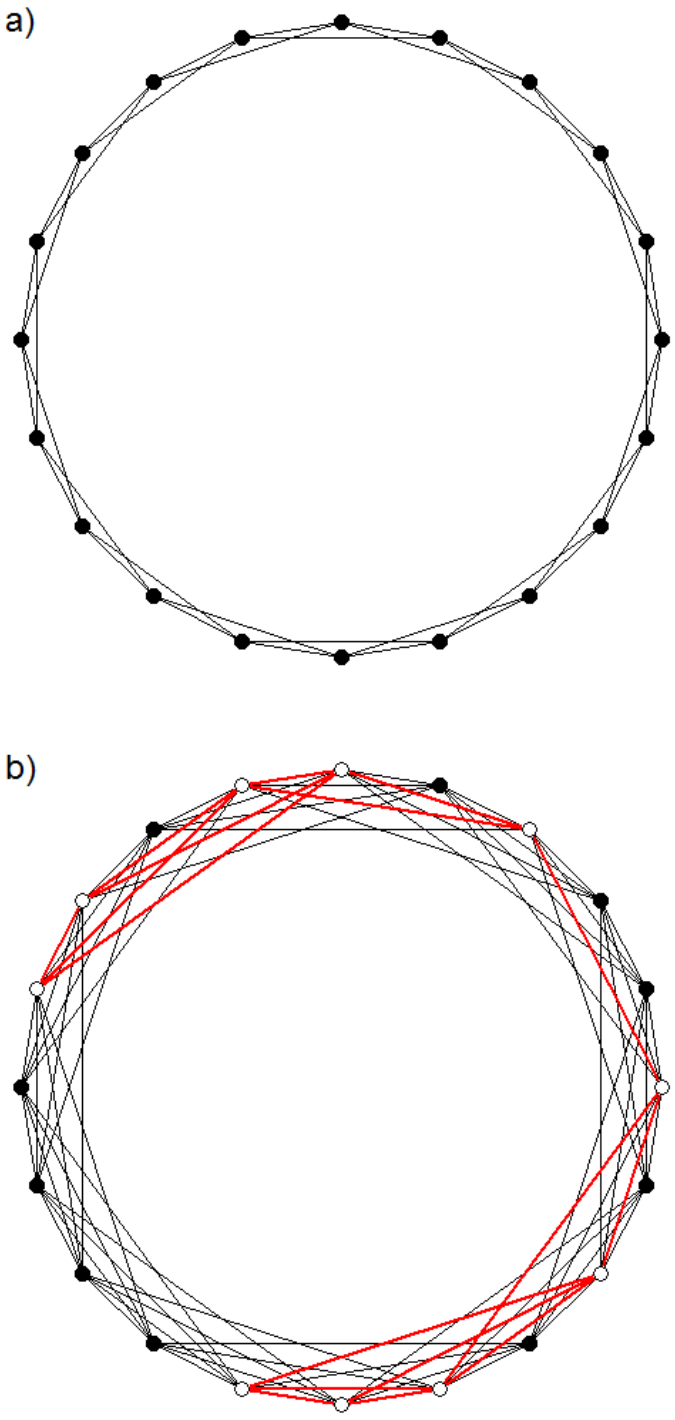

Fig. 5.1. The regular structure of networks containing 20 populations. Black dots represent populations without an Allee effect and white dots represent populations with the strength of Allee effect equal to 1. a) shows a network with 4 connections per population and b) shows a network with 8 connections per population. In a) no Allee effects are operating in any of the populations. In b) 10 populations do not experience Allee effects and 10 populations do. In b) the populations are randomly arranged and the red lines show the connections between populations with the same strength of Allee effects.

All networks consisted of 20 populations and all population time series were run for 10,000 time steps. I selected initial population densities at random from 0.1 to 100 and generated time series for twenty populations to simulate a network absent of dispersers. I repeated this for A= 0, 0.5, 1 and 1.5 using the same initial population densities. These initial population densities were also used to generate all networks of connected populations. To address the question of how connectivity influences synchrony I first varied the strength of connectivity and second the number of connections per population. The strength of connections was the percentage of the resident population dispersing to the adjacent populations and varied from 0.1% to 1.5%. Number of connections per population was 2, 4, 6, 8 or 10 and connections were always to nearest neighbour populations. Both the strength of connections and the number of connections per population was always consistent throughout a network. Again, I repeated this for A= 0, 0.5, 1 and 1.5.

Using the results from the networks varying in connectivity I chose appropriate strengths and numbers of connections that reflected a 'weakly coupled' network to investigate how the strength of Allee effect influences network synchrony. Here, I varied the strength of the Allee effect between networks from 0 to 1.5 with 0.025 intervals, for each given 'weakly coupled' connectivity regime. To explore the impact of varied Allee effects within a network on network synchrony I created 100 networks, each containing 10 populations with an Allee effect (A=1) and 10 populations without an Allee effect (A=0). By randomly selecting from the pool of 20 populations 20 times without replacement for each of the 100 network, I varied the configuration of Allee/Non-Allee populations between networks. Using these randomly generated population configurations I repeated this for networks containing 10 populations with A=0.5 and 10

populations with A=1.5 by replacing all 0 entries with 0.5 and all 1 entries with 1.5. Fig. 5.1. b) shows one example network, of the 100 created, containing 10 populations with A=0 and 10 populations with A=1.

5.2.3. Network Phase Synchrony

The final 500 time steps in each network were analysed to detect cyclic behaviour in the local population dynamics. I did this by identifying repeated series of population densities. The smallest cycle period that satisfied this criterion was recorded for each population. Once I had assigned a cycle period to each of the 20 populations in a network, I calculated the phases for each of their final 500 time steps. After obtaining a set of 500 phases for each population within a network I computed the phase differences between each pair of populations in preparation for evaluating the phase synchrony between any given pair. If the phase difference between population A and population B does not change over the 500 time steps then the populations are in perfect phase synchrony. Conversely, if the phase difference between the populations A and B constantly changes then the two populations show no phase synchrony. To obtain an estimate of phase synchrony between two populations I analysed the distribution of their associated set of phase differences, following the method outlined in Cazelles and Stone (2003) where the Shannon entropy is utilised. By categorising the phase differences into J bins of equal bin width I calculated the Shannon entropy, S, by:

$$S = \sum_{k=1}^{J} p_k ln(p_k)$$

where p_k is the proportion of phase differences in bin k. A Shannon entropy value of 1 represents a uniform distribution of phase differences and, therefore, non-synchronised

phases. To obtain a measure of synchrony, rather than entropy, I used the normalised Shannon entropy (Cazelles and Stone 2003):

$$Q = 1 - \left(\frac{S}{S_{max}}\right)$$

where S_{max} is the largest possible entropy (S_{max} = ln(J)). Here, a Q value of 1 represents perfect phase synchrony. If a population remained at an equilibrium density (including extinction) or did not display cyclic behaviour over the 500 year period, I assigned a Q value of 0 for all population pairs formed with that population. I considered populations as having cyclic behaviour if repeated cycles contained 82 or fewer points per cycle. More points per cycle would have resulted in only a limited number of repeats within 500 year period. As a measure of overall network phase synchrony I used the mean of the Q values for all pairs of populations in a network.

Next, I assessed the relationship between the network phase synchronies produced in networks with different strengths of Allee effect across populations and two network characteristics: the strength of Allee effect corresponding to populations that did not synchronise and the number of connections between populations with the same strength of Allee effect. The former indicates whether one of the two strengths of Allee effect directly is associated with populations not synchronising and the latter indicates the influence configuration of populations had on network phase synchrony. I used a linear regression to test the relationship between network phase synchrony and number of connections between populations with the same strength of Allee effect, for each set of 100 networks. All modelling and analysis was carried out in R version 2.15.2 (R Development Core Team, 2010).

5.3. Results

5.3.1. Local Population Dynamics

Fig. 5.2. a) shows the population densities of the final 3,000 time steps of a time series spanning 12,000 time steps, for varying λ and A=0. When λ is between 1.00 and 2.00 populations reached the carrying capacity of 30 and remained at this density after the initial transient phase which occurred prior to the 9,000th time step. For λ values > 2.00 population dynamics became cyclic, forming 2 point limit cycles up to a λ value of 2.52 and 4 point limit cycles between λ values of 2.53 and 2.65. Larger λ values resulted in 8 and 16 point limit cycles, until λ = 2.70 where population dynamics became semi-chaotic showing densities within restricted bands of density values whilst showing no repeated cyclic pattern. From λ = 2.83 population dynamics were chaotic with density values being limited only between single upper and lower bounds as shown in Fig. 5.2. a). By setting λ to 2.75 I found semi-chaotic behaviour for all A between 0 and 1.5, except a very small subset of A values around 0.93 and 1.36 where cyclic behaviour occurred (Fig. 5.2. b)).

For a population absent of Allee effects just one equilibrium point existed (Fig. 5.3. a)). This point was a stable equilibrium and occurred at the carrying capacity K. As shown in Fig. 5.2. a), for λ=2.75 the population density never actually reached K, instead the density jumped between densities larger and smaller than K depending on where along the solid black line in Fig. 5.3. a) the density of the previous time step existed. For populations experiencing an Allee effect (A>0) two equilibria were present (Fig. 5.3. b-d)). One of these was stable occurring at the carrying capacity K and the other was unstable occurring at x_{t-1} = A. When x_{t-1}< A the log per capita population growth rate was negative indicating population decline. Therefore, if x_{t-1}< A the population would eventually go extinct if isolated from other population sources.

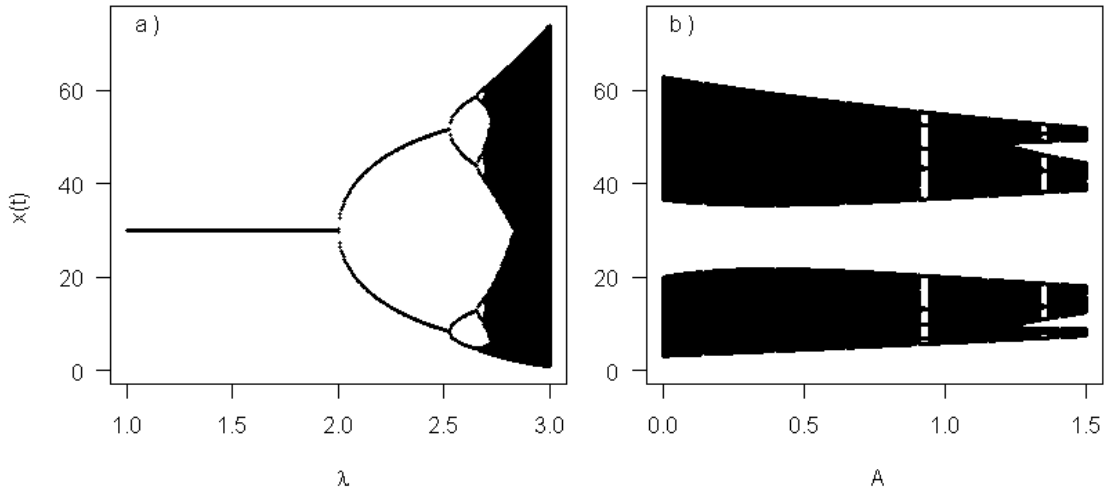

Fig. 5.2. Bifurcation diagrams for λ and A of the Allee equation (Eq. 5.1) used to simulate time series data. A=0 in a) and λ=2.75 in b).

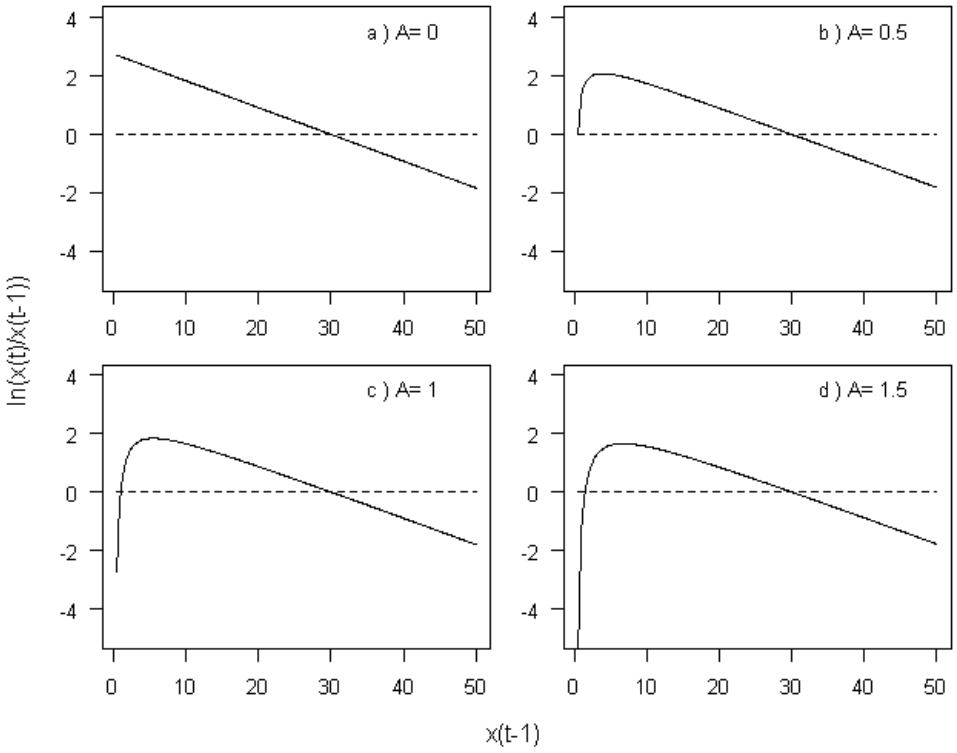

Fig. 5.3. Relationships between per capita growth rate and population density for different strengths of Allee effect.

Initial population densities for populations 1 to 20 were 15.1, 3.9, 31.9, 67.5, 14.9, 26.9, 32.3, 34.1, 28.1, 50.7, 74.9, 28.9, 0.1, 31.3, 57.7, 26.5, 46.1, 3.9, 19.9 and 68.7, respectively, and were the same for all networks created.

5.3.2. Varying Connectivity between Networks

Overall network phase synchrony increased with both strength of connectivity as shown in plots Fig. 5.4. a-c) and the number of connections per population within a network as shown in plots Fig. 5.4. d-f). Increased connectivity is not only shown within each plot but also between plots. As the plots are crossed from a) to c) the number of connections per population is increased and as the plots are crossed from d) to f) the strength of connectivity is increased. Going from plot a) to c) and from plot d) to f) it can be seen that the increase in network phase synchrony occurred at a higher rate, indicating that a combination of both strength and number of connections increased network phase synchrony. The relationships between network phase synchrony and connectivity observed in Fig. 5.4. are not smooth for two reasons, both of which can be explained in terms of the period of cycles. To address this I have plotted the time series for an example population from three networks, each with the same initial population density and location in the network. These three networks had no connectivity (Fig. 5.5. a)), 0.9% strength of connectivity with 2 connections per population (Fig. 5.5. b)), and 0.9% strength of connectivity with 10 connections per population (Fig. 5.5. c)). As the network connectivity increased, this population's dynamics went from semi-chaotic to 8 point limit cycles to 2 point limit cycles. This reduction in cycle period with increased connectivity occurred for all populations, although not all populations would change at the same time. For example, in Fig. 5.4. d) when A=1 network phase synchrony dropped from 0.86 for a

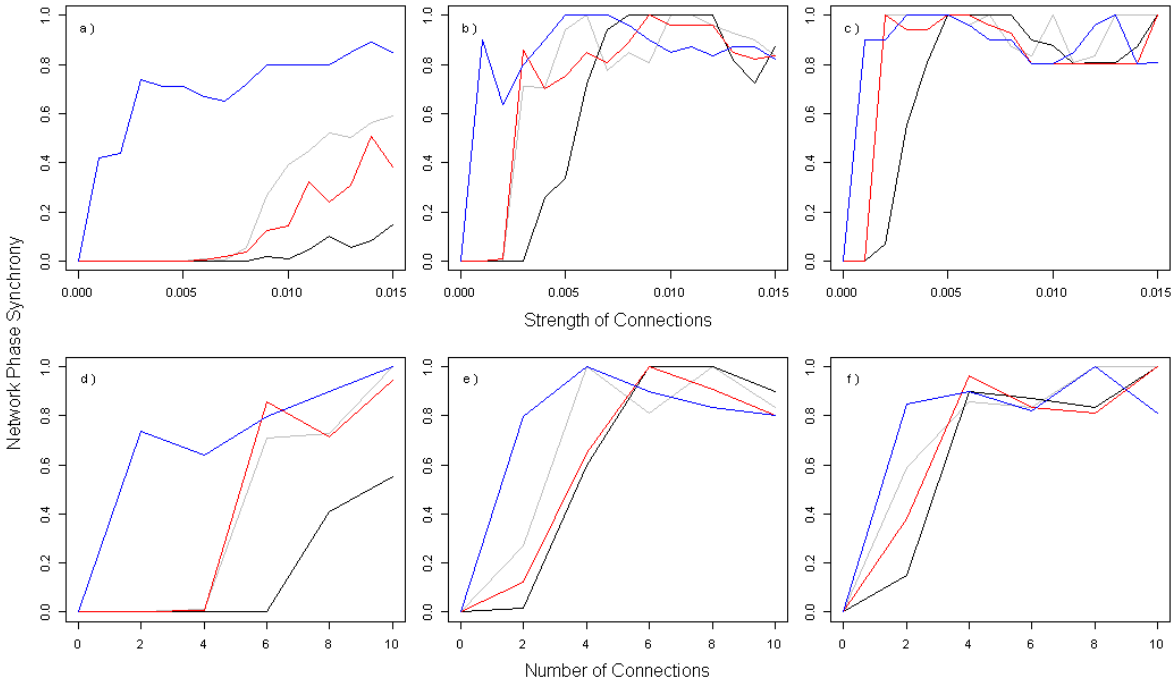

Fig. 5.4. Relationship between connectivity and network phase synchrony for different strengths of localised Allee effects. Plots a-c) show how network phase synchrony varied with strength of connections and plots d-f) show how network phase synchrony varied with number of connections per population. In each plot the different strengths of localised Allee effects within a network are indicated by the coloured lines: A=0, grey; A=0.5, black; A=1, red; A=1.5, blue. Networks contained 20 populations. Each population within a network was connected to their two nearest neighbours in a), their six nearest neighbours in b) and their 10 nearest neighbours in c), and with connection strengths of 0.3% in d), 0.9% in e) and 1.5% in f). (In plots a-c) 0.005, 0.010 and 0.015 are connection strengths of 0.5%, 1.0% and 1.5%, respectively.)

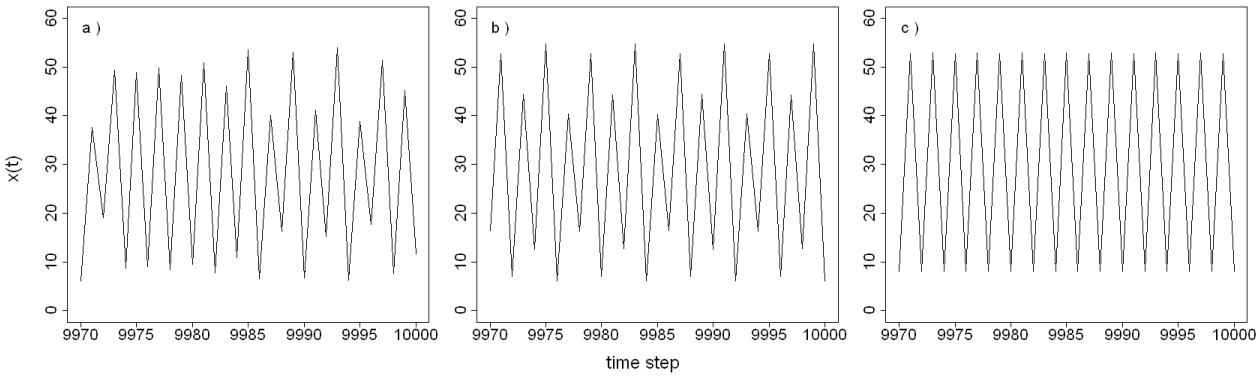

Fig. 5.5. Time series for a population in three networks of constant connectivity that varied between networks. Each of these populations had the same initial population density and network connectivity varied as follows: a) No connectivity, b) 0.9% strength of connectivity with 2 connections per population, c) and 0.9% strength of connectivity with 10 connections per population.

network containing 6 connections per population to 0.72 for a network containing 8 connections per population, and then increased to 0.94 when there were 10 connections per populations. When 6 connections per population existed 18 of the 20 populations had 8 point limit cycles and when 10 connections per population existed 19 of the 20 populations had 4 point limit cycles, which resulted in both networks having high network phase synchrony. In contrast the network with 8 connections per population had 8 populations with 4 point limit cycles and 12 populations with 8 point limit cycles, and therefore a large number of connected populations had low synchrony between one another. This caused the network phase synchrony to be lower than that of the networks with 6 and 10 connections per population. In addition to these decreases in population cycle periods during transitions from all network populations being locked in one cycle period to being locked in another cycle period (as connectivity increased), for other networks, some population cycle periods increased. This was the case in the networks with A=0.5 and 6 connections per population between strength of connections 0.013-0.015 (Fig. 5.4. b)).

5.3.3. Varying Strength of Allee effects between Networks

To investigate how network phase synchrony is influenced by strength of Allee effects in weakly coupled networks I tested networks with 2, 4, 6, 8 and 10 connections per populations, each with strength of connections set to 0.3%. Network phase synchrony had a U shaped relationship with strength of Allee effect for networks with 6, 8 and 10 connections per population (Fig. 5.6.). For these three degrees of connectivity, network phase synchrony increased as A decreased towards 0 and increased towards 1 from the minimum network phase synchronies which occurred between approximately 0.3 and 0.7

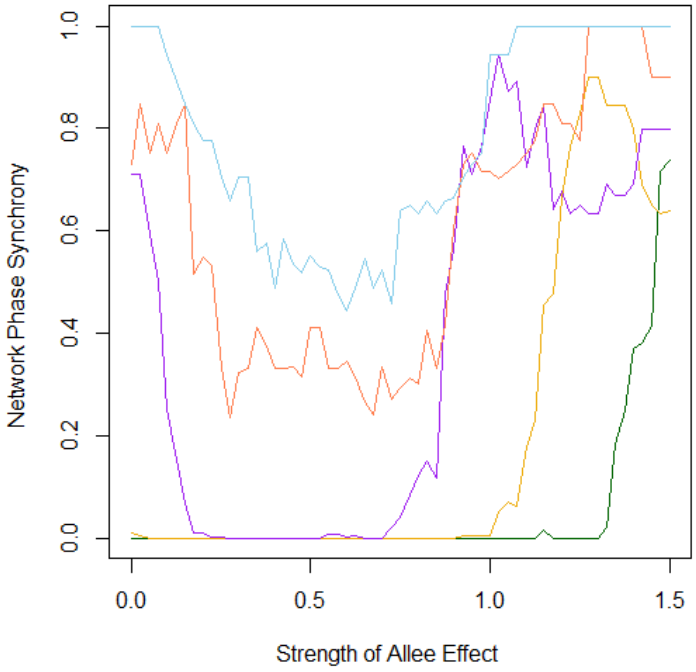

Fig. 5.6. Relationship between strength of localised Allee effects and network phase synchrony for for networks containing a different number of connections per population (cpp) indicated by the coloured lines: 2 cpp – dark green, 4 cpp - gold, 6 cpp - purple, 8 cpp - orange, 10 cpp - light blue. Networks contained 20 populations. Strength of connections within all networks was 0.3%.

(Fig. 5.6.). Network phase synchrony then remained high between A values of 1 and 1.5 for networks with 6, 8 and 10 connections per population and, within this range in A, network phase synchrony fluctuated within a range of 0.31, 0.30 and 0.06 for networks with 6, 8 and 10 connections per population, respectively. The network with A=1.03 and 6 connections per population contained all but one population with 8 point limit cycles. From A=1.05 to 1.50 (for networks with 6 connections per population) a transitioning, analogous to that observed for increased connectivity, occurred whereby populations altered in cycle period as the strength of Allee effect increased, and partially explains the variation in network phase synchrony. A second contributing factor was the extinction of a population with initial population density of 0.1. This population went extinct in all networks where A=1.13 to 1.50. Similarly, for networks with 8 connections per population, transitioning occurred in networks with A values between 1.00 and 1.50, and the population with initial density of 0.1 went extinct where A = 1.45 to 1.50. No populations went extinct in any networks with 10 connections per population.

Network phase synchrony was below 0.02 between A values of 0.05 and 1.03 for networks with 4 connections per populations and between A values of 0.00 and 1.33 for networks with 2 connections per population. As A increased above 1.03 and 1.33 for networks with 2 and 4 connections per population, respectively, network phase synchrony remained relatively high.

5.4.3. Varying Population Configuration between Networks

For this section I set strength of connectivity to 0.3% and the number of connections per population to 8. The mean network phase synchrony, standard deviation and median network phase synchrony were 0.70, 0.05 and 0.71 for the set of 100 networks with A

values of 0 and 1, and 0.42, 0.14 and 0.41 for the set of 100 networks with A values of 0.5 and 1.5 (Fig. 5.7.). To investigate why these distributions of network phase synchrony were produced I assessed two possible contributing factors. The first was the strength of Allee effect corresponding to populations that did not synchronise, i.e. populations that either did not lock into cycles of the same period as any other populations in the network or did not display cyclic behaviour at all. Over the 100 networks with A values of 0 and 1, there were 9 instances where cyclic behaviour was not detected in one population (initial population density = 3.9), 8 instances in another (initial population density = 68.7) and 1 instance in a third population (initial population density = 26.9). In one network all three of these populations did not synchronise and in 8 networks two of these populations did not synchronise, leaving one instance of non-cyclic behaviour which occurred in a network of otherwise cyclic population behaviours. All instances of non-cyclic behaviour corresponded with an A value of 0 in the population for which 9 instances where found, and all instances of non-cyclic behaviour corresponded with an A value of 1 in the population for which 8 instances where found. By contrast, over the 100 networks with A values of 0.5 and 1.5 there were a total 376 instances where cyclic behaviour was not detected, 364 of which corresponded to populations with A=0.5 and only 12 corresponded to populations with A=1.5. Only two populations displayed cyclic behaviour in all 100 networks when A values were 0.5 and 1.5.

The second possible contributing factor assessed was the number of connections between populations with the same strength of Allee effect. A total of 80 connections existed within these networks of 8 connections per population, i.e. 160 dispersal events per time step as individuals dispersed in both directions between connected populations with the predefined strength of connection for each direction (Fig. 5.1 b). Number of

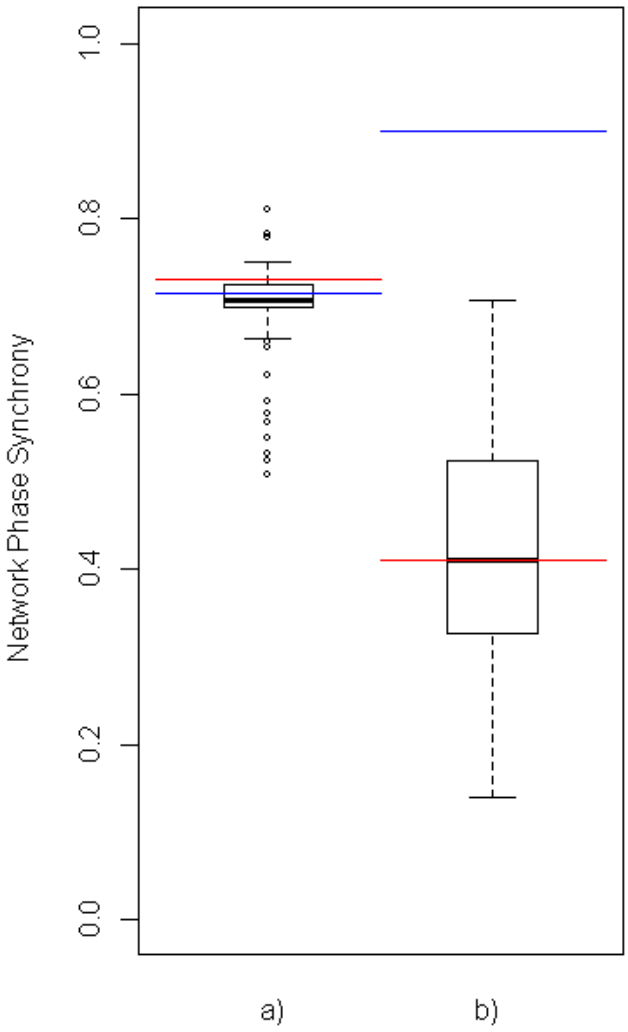

Fig. 5.7. Distribution of network phase synchronies for networks differing in population configuration. Each network consisted of 10 populations with one strength of Allee effect and 10 populations with a different strength of Allee effect. For a) these strengths were 0 and 1, and for b) these strengths were 0.5 and 1.5. 100 networks of differing population configuration were tested in each. Red lines corresponds to the network phase synchrony for a network with the same connectivity and all network populations with A=0 in a) and all network populations with A=0.5 in b). Blue lines corresponds to network phase synchrony for a network with the same connectivity and all network populations with A=1 in a) and all network populations with A=1.5 in b).

connections between populations with the same strength of Allee effect did not significantly affect network phase synchrony in either set of 100 networks (Networks with A values of 0 and 1: t=-0.445, df=98, p=0.658; networks with A values of 0.5 and 1.5: t=-0.623, df=98, p=0.535).

5.4. Discussion

Here I showed that network phase synchrony increased with connectivity for networks of given strength of localised Allee effect. This result concurs with studies that have found the same relationship in networks that do not contain Allee effects (Watts & Strogatz, 1989; Pecora & Carroll, 1990; Kendall, 2000; Holland and Hastings, 2008). Above a threshold connectivity, network phase synchrony remained relatively high. There was some variation in these overall observed relationships which can be explained by transitioning stages. When connectivity was increased the cycle period in localised population dynamics would decrease, although not all populations would change in their cyclic behaviour. This caused the appearance of transitioning stages where certain pairs of populations that were previously cycling with the same period, would desynchronise as one changed in cycle period and the other remained the same. The resultant network phase synchrony depended on the number of populations changing in one interval of increase in connectivity, and on the phase difference between the phases of a population's new cycle period and the phases of connected populations' cycle periods.

The relationship between network phase synchrony and strength of Allee effect varied with connectivity. For networks with weak strength of connections a U shape relationship was displayed when 6, 8 or 10 connections per population were present, but when fewer connections existed no (or occasionally little) network phase synchrony was

observed for very small A values. As connectivity increased, the population with a small initial density of 0.1 went extinct in networks with higher strength of Allee effects suggesting that increased connectivity could potentially prevent the extinction of vulnerable populations when strength of Allee effects is relatively high. Again, transitioning stages were found and were responsible for the variation in network phase synchrony observed over small ranges of Allee effect strength.

The results for the final part of my analysis raise a number of interesting questions, as the two scenarios I have tested showed huge disparity in distributions of network phase synchronies and provided little information about why this disparity exists. For the purpose of this discussion I'll call the set of 100 networks that contained 10 populations with strength of Allee effects of 0 and 10 populations with strength of Allee effects of 1 as set A, and the set of 100 networks that only differed from set A by strengths of Allee effect as set B. Set B had exactly the same configuration of populations as set A - wherever a population had a strength of Allee effect equal to 0 in set A the same population had 0.5 in set B and wherever a population had a strength of Allee effect equal to 1 in set A the same population had 1.5 in set B. Set A showed relatively little variation in network phase synchronies compared to set B. In both sets the average (mean and median) was very similar to the network phase synchrony for the network in which the lower A value was consistent across all populations (Fig. 5.7.). Populations in the network with A=0 across all populations had a similar level of synchrony as populations in the network with A=1 across all populations (Fig. 5.6., orange line), and in both cases populations are driven into a similar proportion of 4 and 8 point cycles. This suggests that, for the degree of connectivity present in these networks, the forces driving synchrony are similar when A=1 and A=0. By contrast, the network phase synchrony for

the network with A=0.5 across all populations was very different to that for A=1.5 (Fig. 5.6., orange line). From these results I hypothesise that the variation in a set's distribution of network phase synchronies is influenced by the difference in network phase synchronies observed for the two networks in which each A value is consistent throughout the network (as indicated by the blue and red lines in Fig. 5.7.). I also hypothesise that a set's average network phase synchrony corresponds to the lower of the two network phase synchronies associated with the A values. Analysing more sets with different pairs of A values would be necessary to test these hypotheses.

There was no clear pattern in populations that did not synchronise. In set A there were two populations that frequently did not synchronise across the 100 networks suggesting that there is a specific feature associated with these two particular populations that caused them to be less susceptible to synchronisation but their initial population densities, which are the only features that could differentiates them from other populations, were the same as or very similar to the 18 other populations and not similar to one another. There was therefore no evidence to suggest that initial population density was responsible for these two populations being less susceptible to synchronisation. Interestingly, non-synchrony always corresponded to A=0 for one population and always corresponded to A=1 for the other population. Although, this pattern was not mirrored in set B where 364 of the 376 instances of populations not synchronising occurred when A = 0.5. It is therefore very difficult to draw any conclusions about relationships between certain strengths of Allee effects and non-synchronising populations in these networks. Again, testing more scenarios with networks of differing strengths of Allee effect will help shed light on this matter.

The variation in network phase synchrony for set A and for set B was not explained by the configuration of populations, as measured by the number of connections between populations of the same strength of A. This implies that in networks with a simple regular structure the populations contribute equally to the network phase synchrony as the arrangement of populations with differing strengths of Allee effect does not significantly alter network phase synchrony. This raises the question: how does network structure affect population synchrony? There has been extensive work carried out on complex networks spanning a whole host of biological systems such as brain networks and food webs (Costa *et al.* 2011). Small world networks are a specific type of complex networks which attempt to mimic the structure of real world systems by adopting a structure that lies somewhere between completely regular and completely random structures, and have been applied to a number of ecological problems (Watts & Strogatz 1998; Holland & Hastings 2008; Goldwyn & Hastings 2011). I could extend this current study of the influence of Allee effects on network synchrony by applying the small world networks approach, replacing the regular structure I have used with a more complex structure that mimics wild animal metapopulation structures.

In this chapter I have used a measure of network phase synchrony, extended from the measure of population phase synchrony defined by Cazelles & Stone (2003), to explore the influence of Allee effects on network synchrony. This measure of network phase synchrony has proven to be useful in this study, not only for extracting info about influencing variables, but also in terms of identifying transitioning stages as these variables change. I found that as network connectivity increased network synchrony increased for different strength of localised Allee effect. I also identified the relationships between strength of Allee effect and network synchrony for five different network

connectivity regimes. It is clear from the final section of my analysis that more work is needed to understand the synchronicity of populations in networks made up of populations varying in strength of Allee effects. This future work should include testing more scenarios that consider more pairs of strengths of Allee effects and alternative network structures that take advantage of the small world network approach. Completing these two extensions would provide a much clearer understanding of the impact Allee effects have on synchrony in wild metapopulations across which Allee effects are not consistent throughout, as was suggested by the distributions of populations displaying Allee effects across species' ranges in Chapter 4.

Chapter 6: Discussion

Small populations face a high risk of extinction for multiple reasons including demographic and environmental stochasticity. Stochasticity is random variation and cannot be predicted. An Allee effect is a density-dependent process that may drive small populations to extinction, and a number of approaches can be utilised to investigate the impact Allee effects have on wild populations. Three of my four research chapters focus on the detection of Allee effects in wild butterfly populations, while my final research chapter explores the impact of Allee effects on network (metapopulation) synchrony. In my thesis I have dealt with the problems associated with detecting Allee effects using both frequentist and Bayesian statistical analyses.

Few studies consider the spatial variation in localised population dynamics, focusing either on the dynamics of a single population that is part of a wider metapopulation or averaged dynamics across a wide area, e.g. a species' range. These approaches are often useful for unveiling general trends in species abundances and can provide valuable information about the conservation status of a species, directing research effort towards species most at risk of extinction. However, approaches that do not investigate spatial variation could result in important ecological processes going unidentified and their impact on a species population dynamics being misunderstood. In chapter 2 I identify spatial variation in the drivers of large skipper *Ochlodes sylvanus* population dynamics across its British range. I show that density-dependent processes and density-independent weather factors vary qualitatively across space. While weather is known to play a key role in butterfly biology and population dynamics, its relative importance in comparison to density dependence has not been demonstrated. In this

study I estimate this relative importance and show how it varies across the British range of *O. sylvanus*. I found that in four (out of twenty-one) 100 km square regions weather is more influential than density dependence to population dynamics, and that these four regions are clustered in North Wales and North West England (Fig. 2.3). The relative importance of density dependence was greater than weather in all other analysed regions, and appeared to increase in relative importance as the range of *O. sylvanus* is crossed from North West to East.

In this study I detected Allee effects in two *O. sylvanus* 100 km square region, although from this analysis the extent to which Allee effects play a role in governing this butterfly's population dynamics is unclear. In order to evaluate the influence of Allee effect fully local population level analyses were necessary. However, the impact of weather also varies across space (as demonstrated in chapter 2) and therefore analysis of local population level density dependence would require the consideration of a number of weather variables. As there are many potentially weather variables important for butterfly population dynamics, local population level analyses would require the inclusion of a large number of variables which would not have been possible given the data available. Issues also arise from the presence of observation errors in population data, which can lead to inaccuracies in results from population analyses (Freckleton *et al.* 2006).

To reduce these limitations, in chapter 3 I developed a Bayesian approach for detecting local population level Allee effects. By using Bayesian hierarchical models I partitioned out the error associated with butterfly data collection (observation error) and the error associated with influential factors that are not included in the density-dependent process part of my models (process error). Process error includes weather,

and other external factors, affecting population dynamics, and its inclusion meant that weather factor did not need to be explicitly included in the models. The inclusion of observation error provides higher confidence, compared to analyses that exclude observation error, in the detection of Allee effects (and negative linear density dependence) when analysing data using this Bayesian approach. In chapter 4 I implement this Bayesian approach to investigate the prevalence of Allee effects within and across British butterfly species. I found that 35 out of the 37 species analysed displayed local population level Allee effects. Little is known about the prevalence of Allee effects in natural populations, and this study therefore provides an extremely valuable example of the frequency to which Allee effects can occur.

I examined a species' susceptibility to Allee effects using the proportion of its total populations that displayed Allee effects as a measure of susceptibility. I tested five species traits relating to mate location and dispersal, as these have been shown previously to drive Allee effects in other butterfly species. None of these five traits significantly influenced susceptibility to Allee effects. However, I did find that susceptibility to Allee effects was significantly affected by phylogeny, which to my knowledge is the first time a link has been made between Allee effects and phylogeny through comparative analyses. More generally, my work highlights the importance of phylogeny on population dynamics, and emphasizes the need to consider phylogenetic relatedness in population dynamics studies. From my results I was able to identify specific groups of closely related species that showed similar susceptibility to Allee effects (for example closely related Nymphalidae *Argynnis aglaja, Argynnis adippe, Argynnis paphia* and *Limenitis camilla* had similar and relatively high susceptibility to Allee effects). Identifying groups with similar susceptibility to Allee effects may allow predictions to be

made about other species. Such species could include those that are endangered and/or rare, for which little population data exists.

In chapter 5 I found that Allee effects play an important role network synchrony. This theoretical study revealed complex relationships between synchrony and strength of Allee effect, however, in networks of a fixed low dispersal, I found that phase synchrony ranged from 0 at relatively low strength of Allee effects to over 75% population synchrony for networks with no Allee effects and for networks with relatively strong Allee effects.

In summary, my work has contributed to various areas of population ecology and I hope that future work can build on my findings. In particular, the prevalence of Allee effects across more taxa as this is vital to understanding the contribution Allee effects have on global species extinctions. Additional comparative analyses in other taxa would also provide more information about the mechanisms driving the link between phylogeny and Allee effects found for British butterflies. Extended evaluation of susceptibility to Allee effects for closely related species may also allow predictions about the influence of Allee effects in rare and/or endangered species. My results suggest that nectar plant mating location sites may be a contributing factor in alleviating Allee effects. Future assessment of resource based aggregated mating systems may guide analyses of certain mating behaviours. Finally, the theoretical work I carried out raised a number of questions and indicates that many more network scenarios need to be investigated to tease apart the influence Allee effects have on network synchrony. These scenarios may include realistic networks structures using a small world approach.

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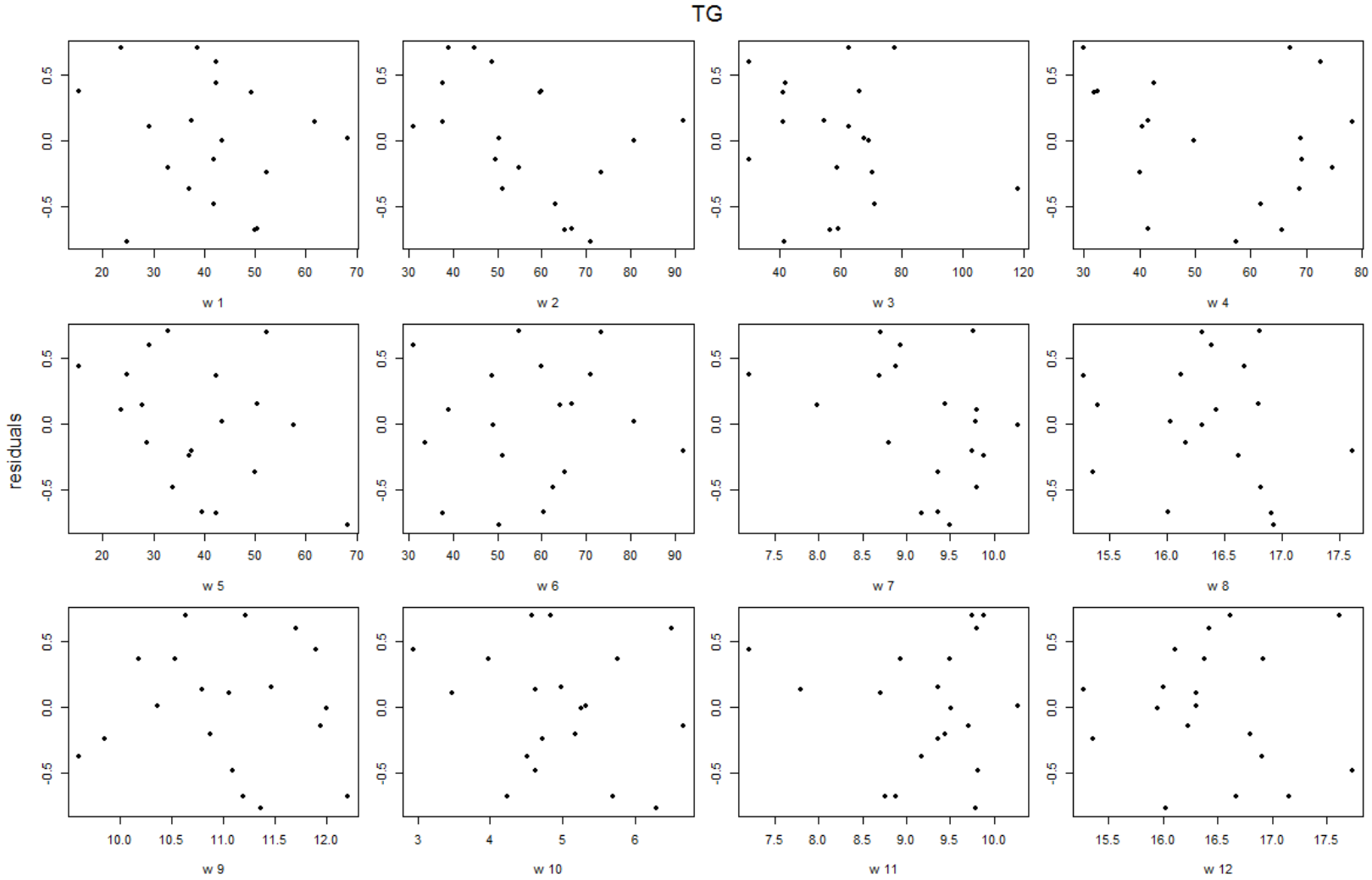
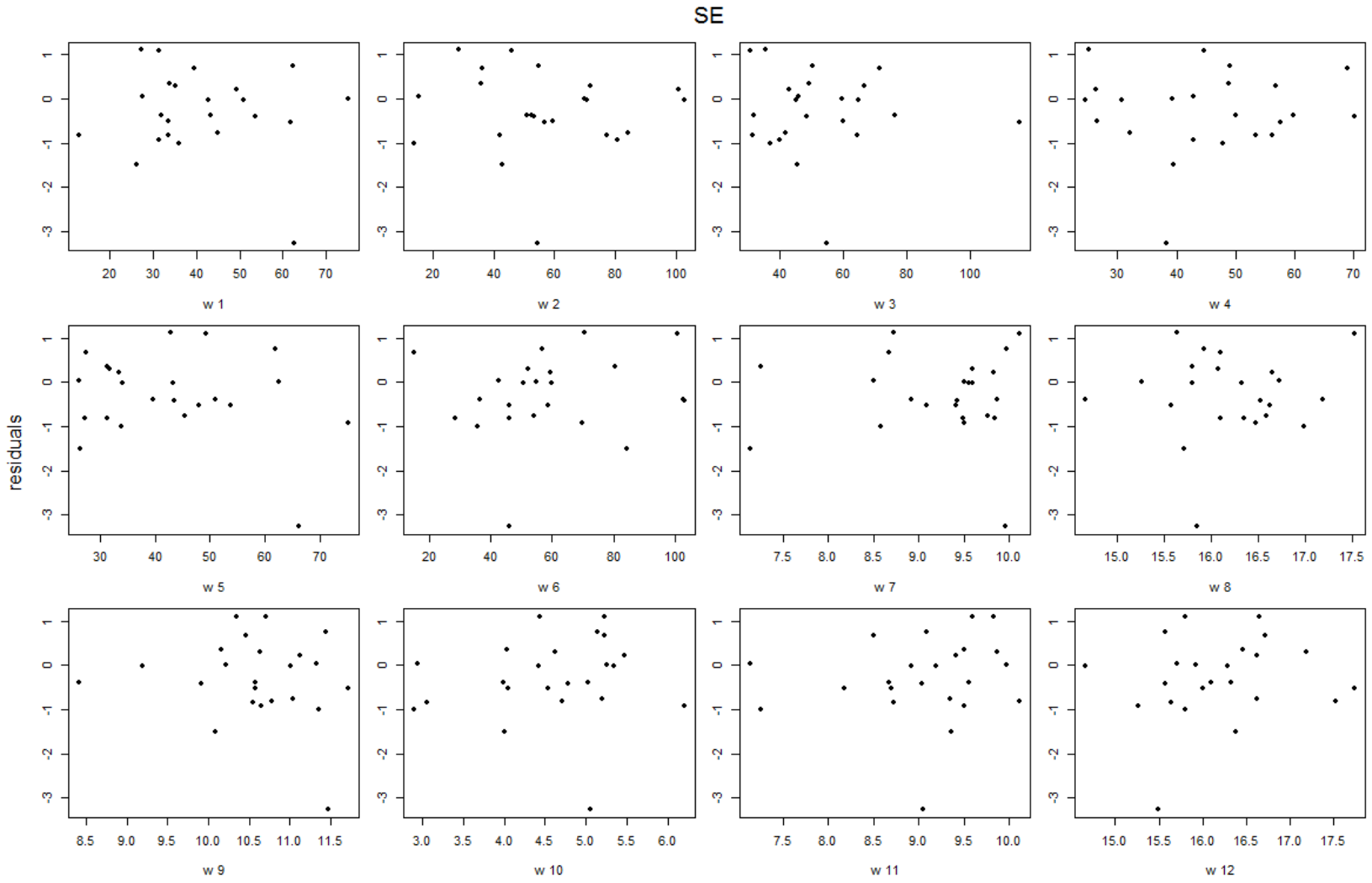
Appendix A

Table A.1. Intercept, coefficients and p-values of significant terms affecting log per capita growth rate in each 100 km square region's minimum adequate model (section 2.3.). The two letters used by Ordinance Survey National Grid to identify each grid square are reported as 100 km square Region ID. X_{t-1} is previous year log population density. W_1, W_2, W_3, W_4, W_5 and W_6 are the mean rainfalls of previous year's spring (March, April, May), previous year's summer (June, July, August), previous year's autumn (September, October, November), current year's winter (previous year's December, January, February), current year's spring, and current year's summer, respectively. W_7, W_8, W_9, W_{10}, W_{11} and W_{12} are the mean temperatures of previous year's spring (March, April, May), previous year's summer (June, July, August), previous year's autumn (September, October, November), current year's winter (previous year's December, January, February), current year's spring, and current year's summer, respectively. The sign of intercepts and significant term coefficients are expressed using + for positive numbers and – for negative numbers. The p-value for each significant term is expressed as follows; ^ p>0.1, * p<0.05, ** p<0.01, *** p<0.001

100 km square Region ID	Mean Log Density	Intercept	X_{t-1}^2	X_{t-1}	W_1	W_2	W_3	W_4	W_5	W_6	W_7	W_8	W_9	W_{10}	W_{11}	W_{12}
TG	-5.43	-*	-*	-*												
SE	-6.43	-														
SS	-7.64	-**	-**	-***							-*					
SH	-6.65	+	+**	+*	+*		-**					+***			-*	
NZ	-6.76	-***		-**					+*							
SJ	-6.10	-**	-*	-**		-***								+*		
TM	-7.42	-		-***				-***					-*	+**	-**	+**
SN	-7.22	+*		-***		-*		-*					-**			
SX	-6.95	-*		-**		-*										
SK	-6.39	-		-***									-*			
TF	-6.01	-***		-***												
TR	-6.03	-***		-***												
SY	-6.21	+**	+*	+					-*				-**		-*	
SD	-6.58	+		-***	+**	-**			+**	-**						-*
SZ	-5.86	-***		-***		+*										
SO	-5.65	+	+*	+	+**				-**				-**		-*	
SP	-5.42	-		-***	+**								-*		-**	
TL	-6.38	-***		-***					-**	-*				-**	+*	
ST	-6.07	+		-***			+*					-***			-**	+*
TQ	-6.48	-**		-***	+***		-***						-***	-**		
SU	-6.04	-***		-***	+***		-***			-***			-*	-***		

Fig. A.1. Scatter plots of weather variables *vs* residual per capita growth rate for each 100 km square region of the large skipper's British range (section 2.2.2.). At the top of each panel of 12 weather plots is the region's OS grid reference. W1-W12 are as stated above in Table A.1. The residual per capita growth rates are the adjusted growth rates after accounting for significant density dependent terms.

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residuals
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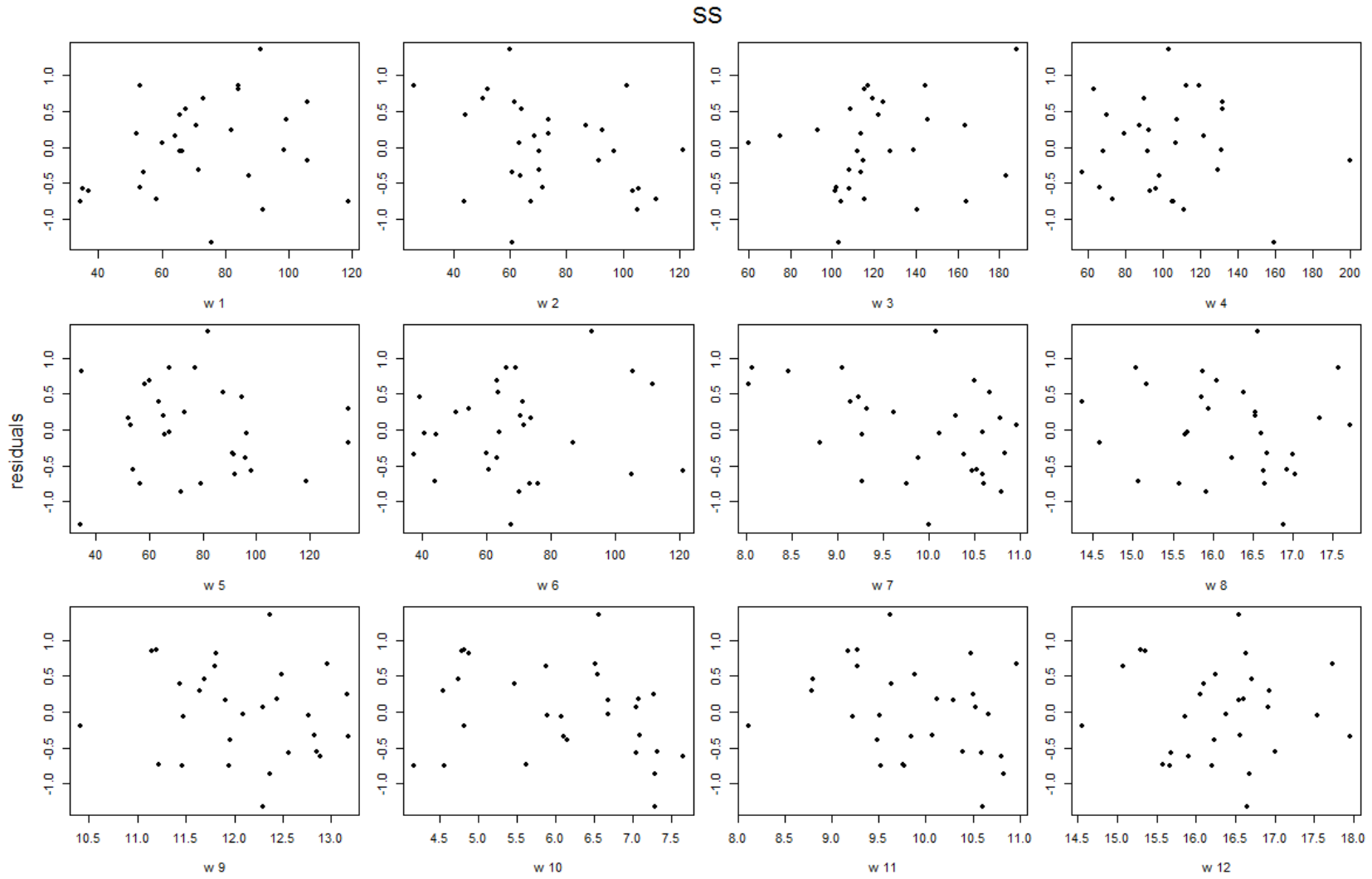
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residuals
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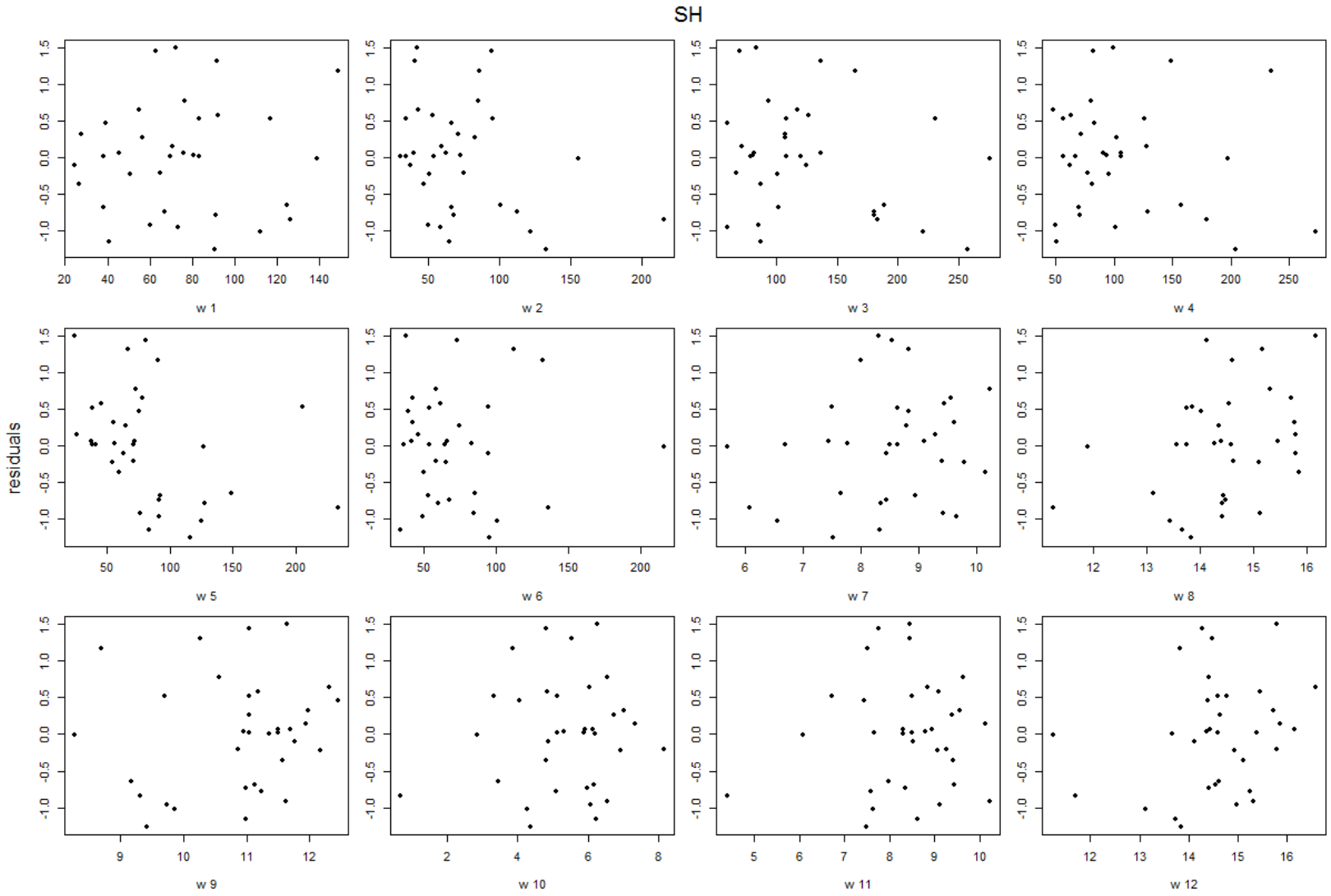
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residuals
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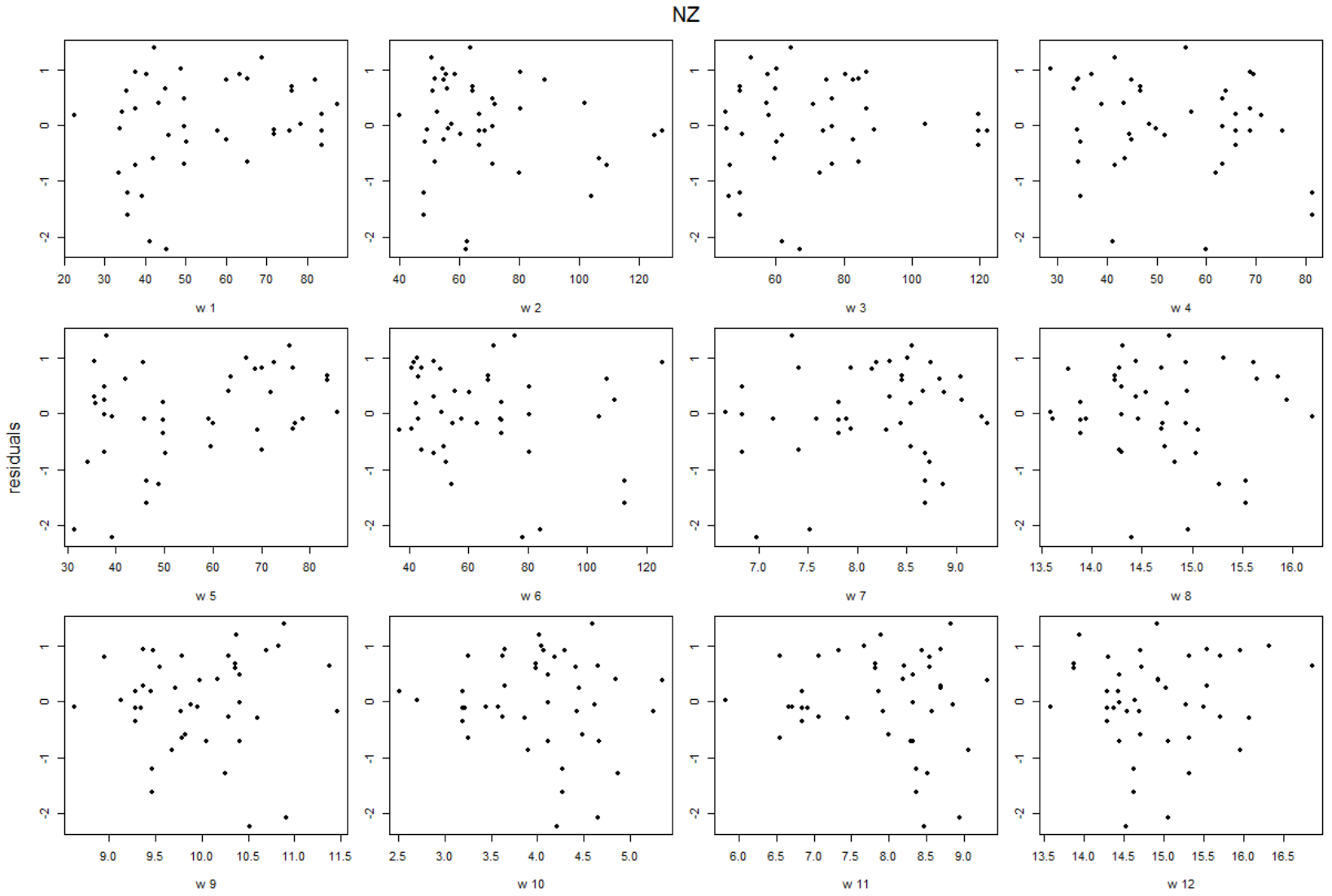
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residuals
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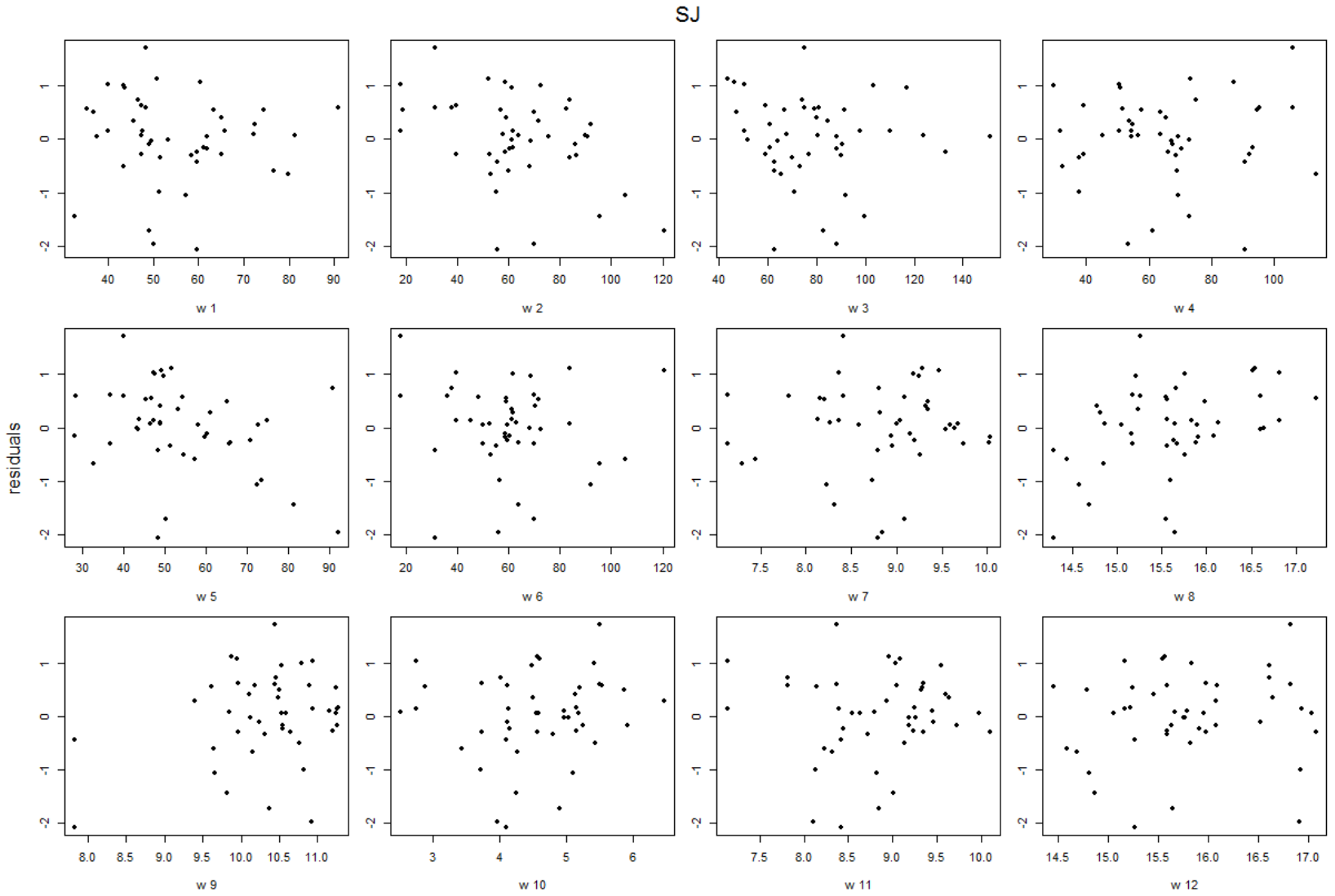
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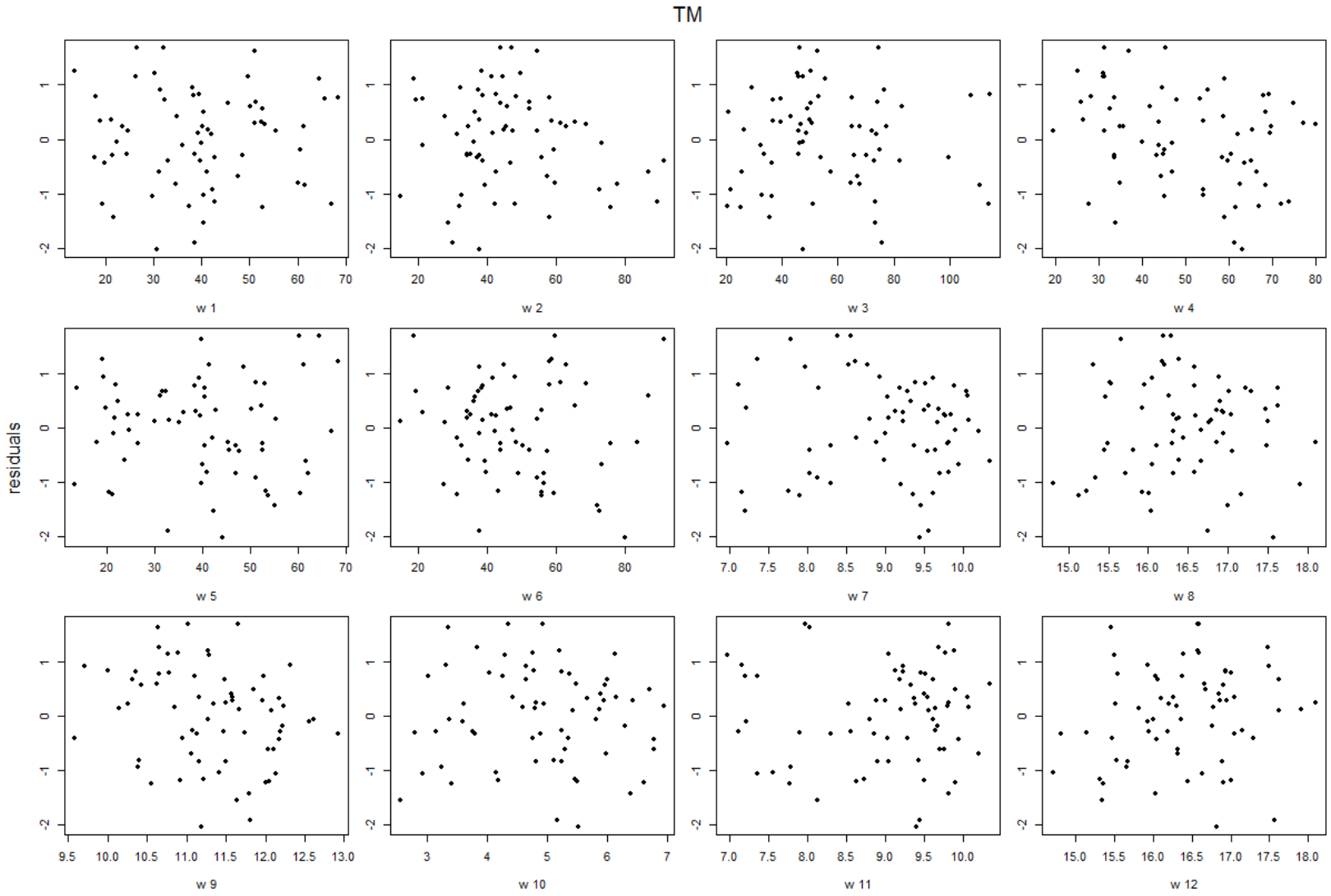
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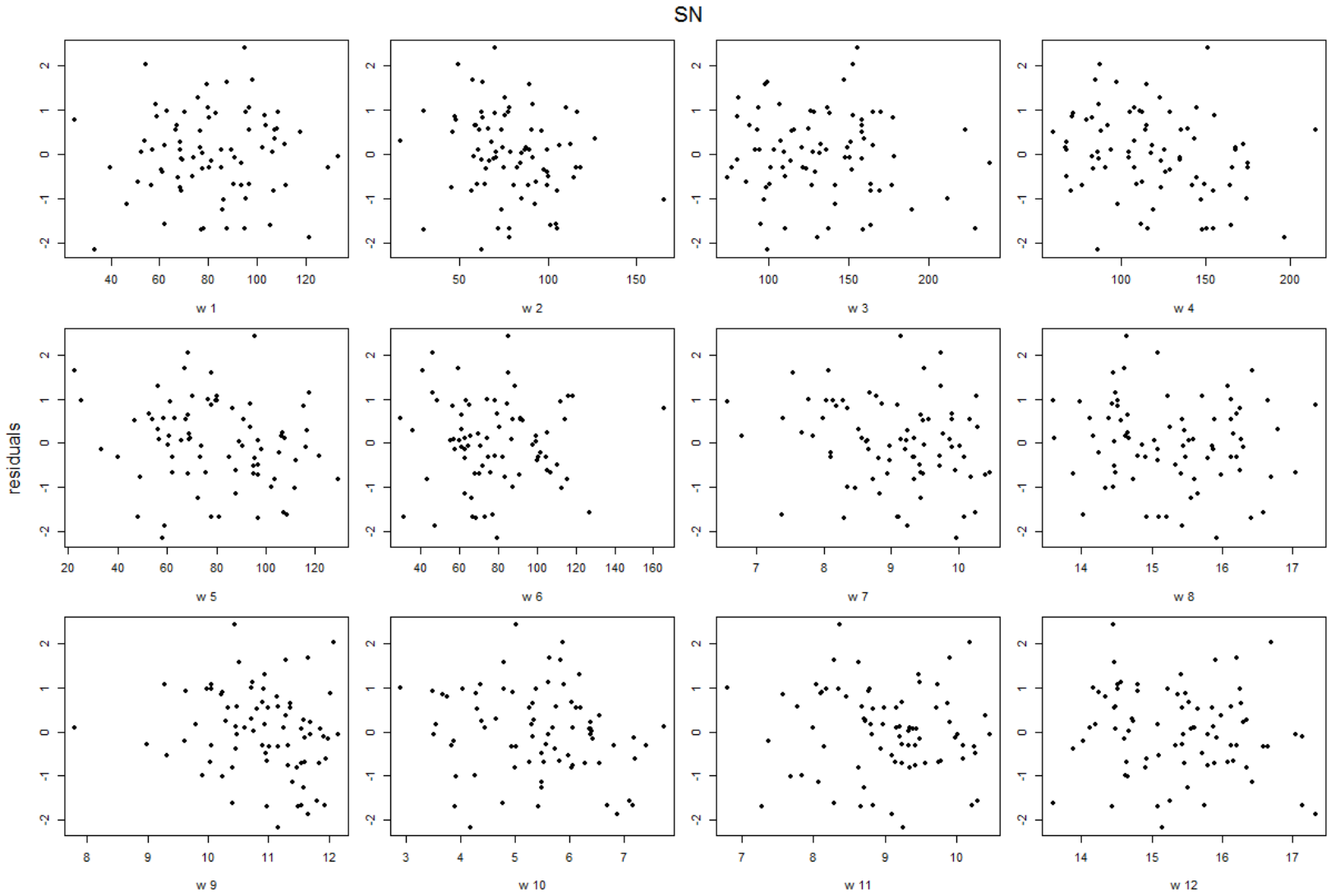
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residuals
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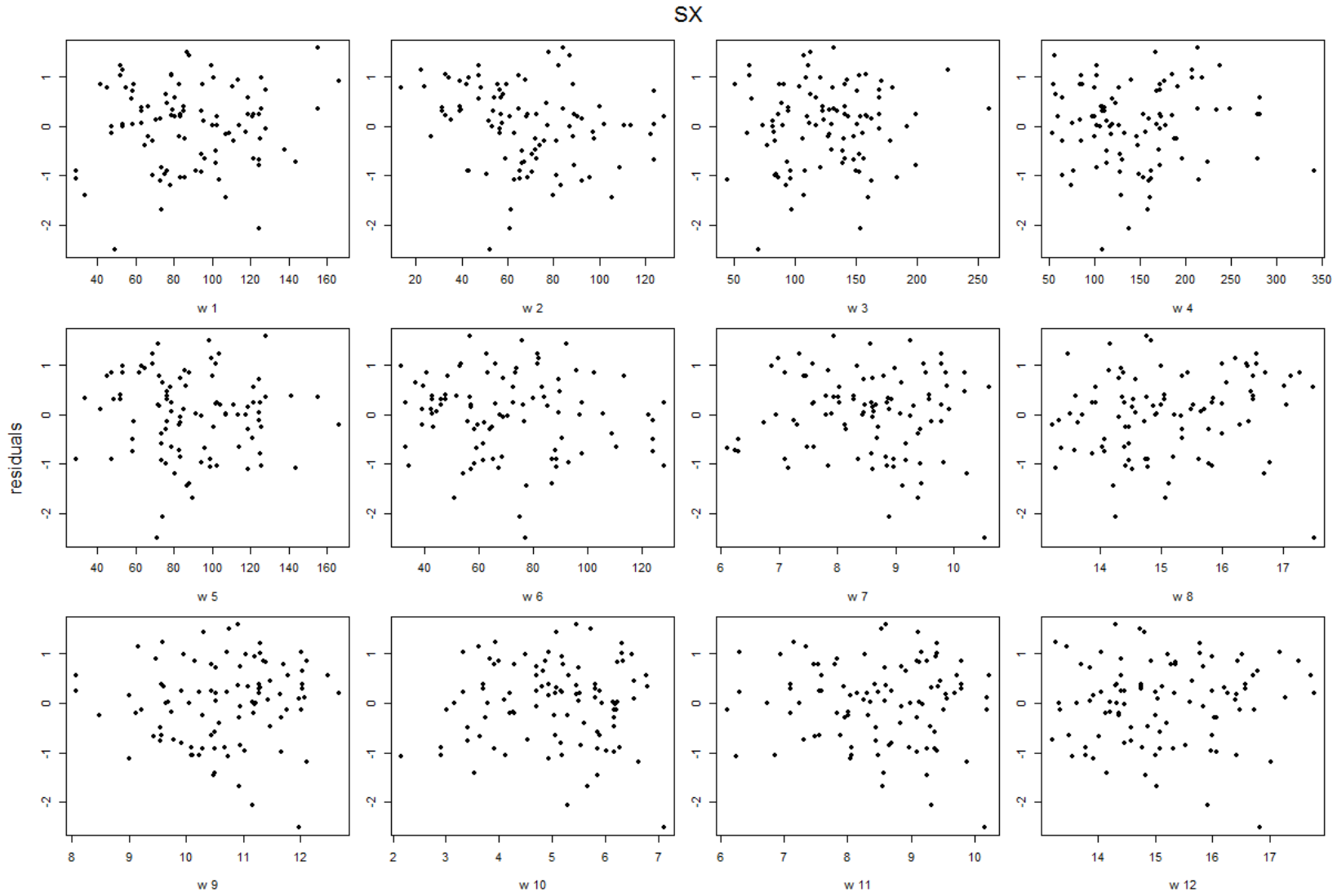
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residuals
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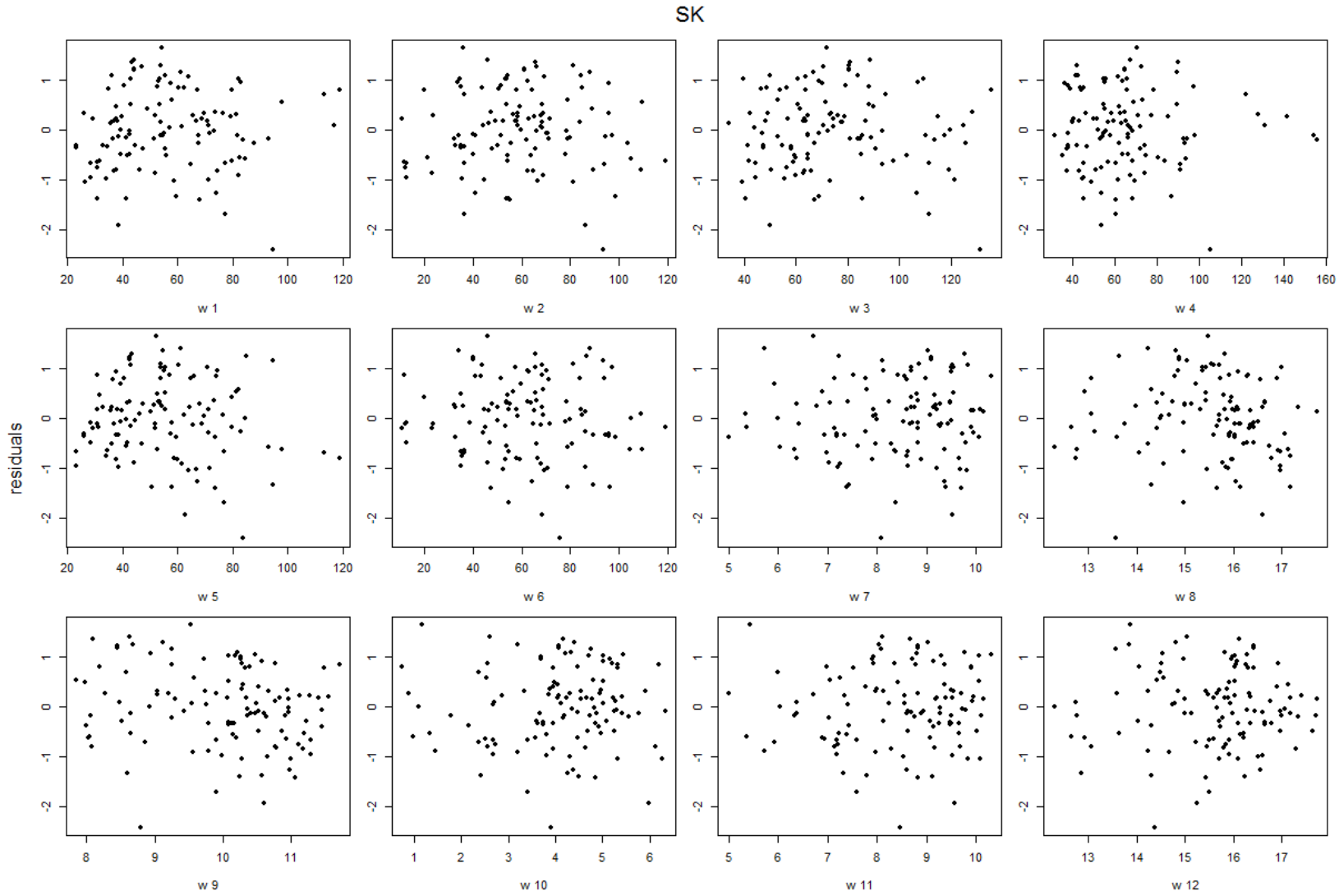
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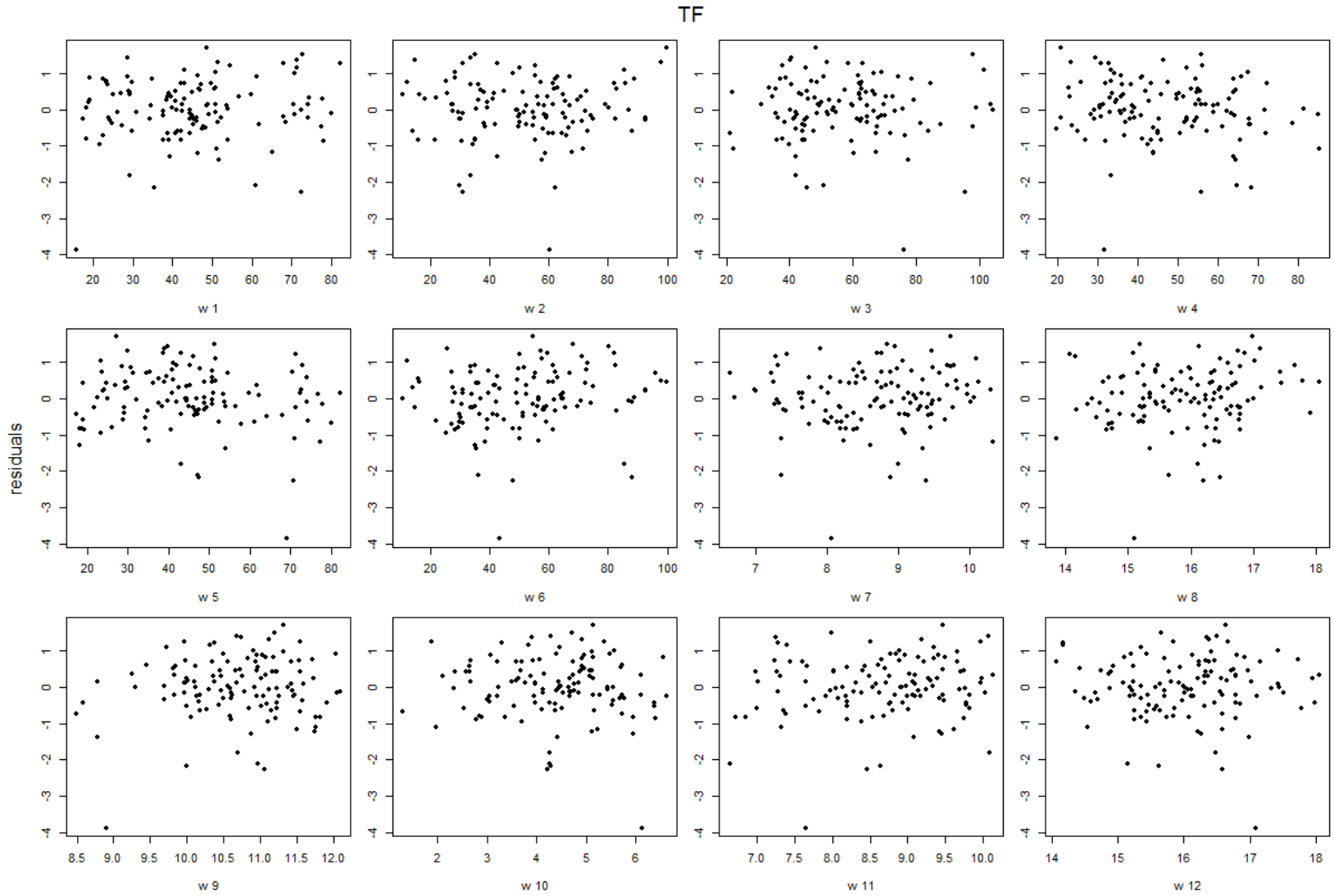
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residuals
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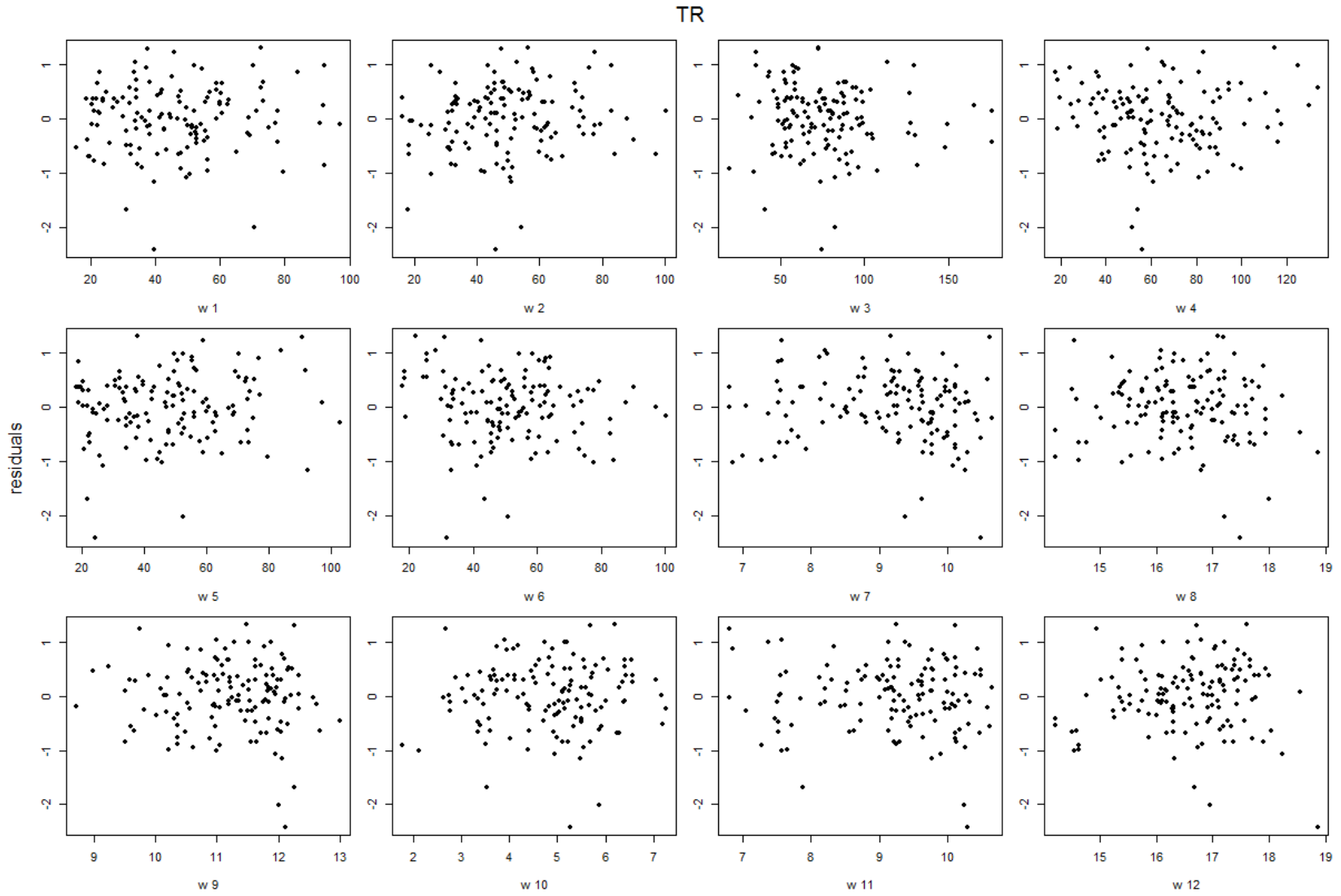
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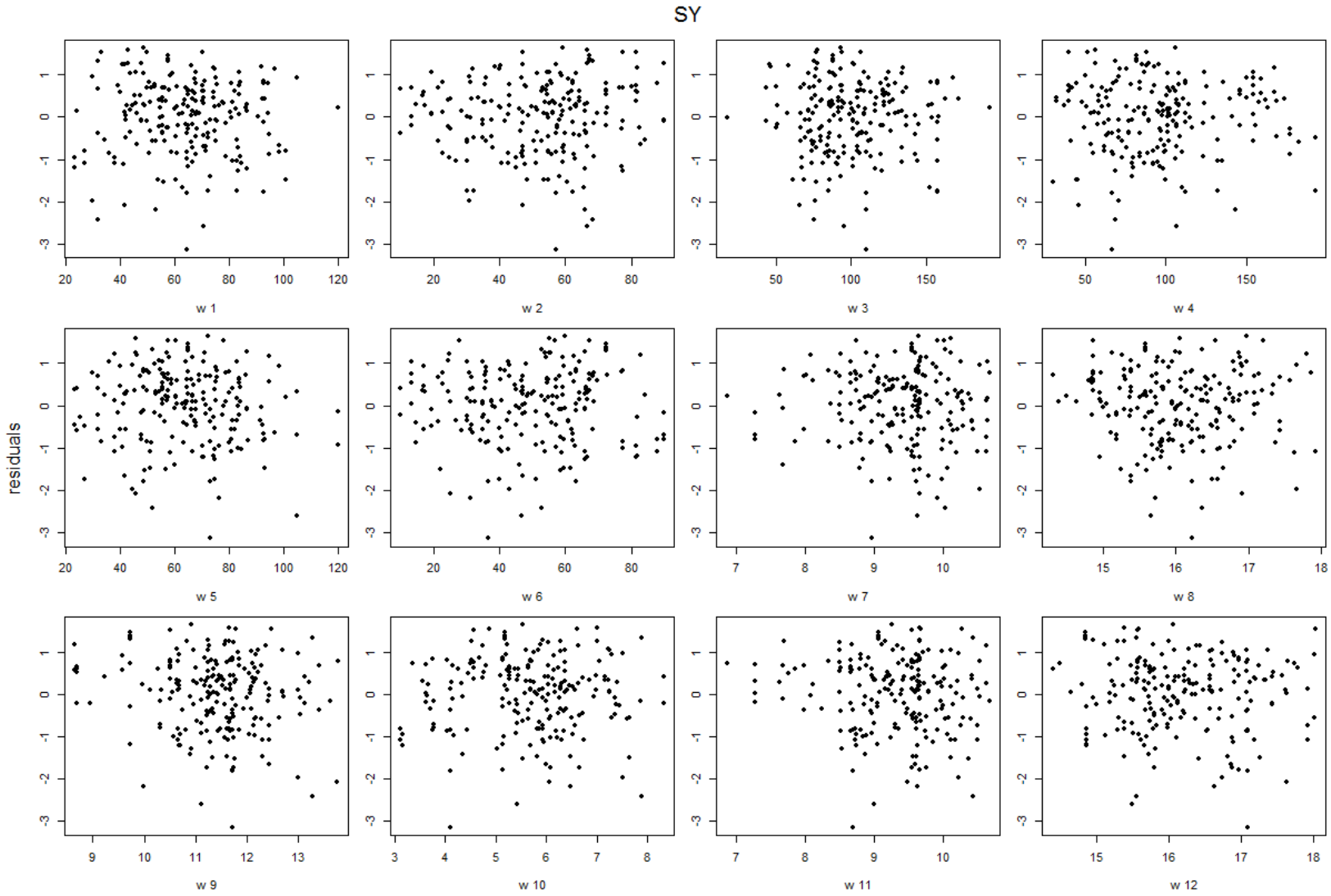
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residuals
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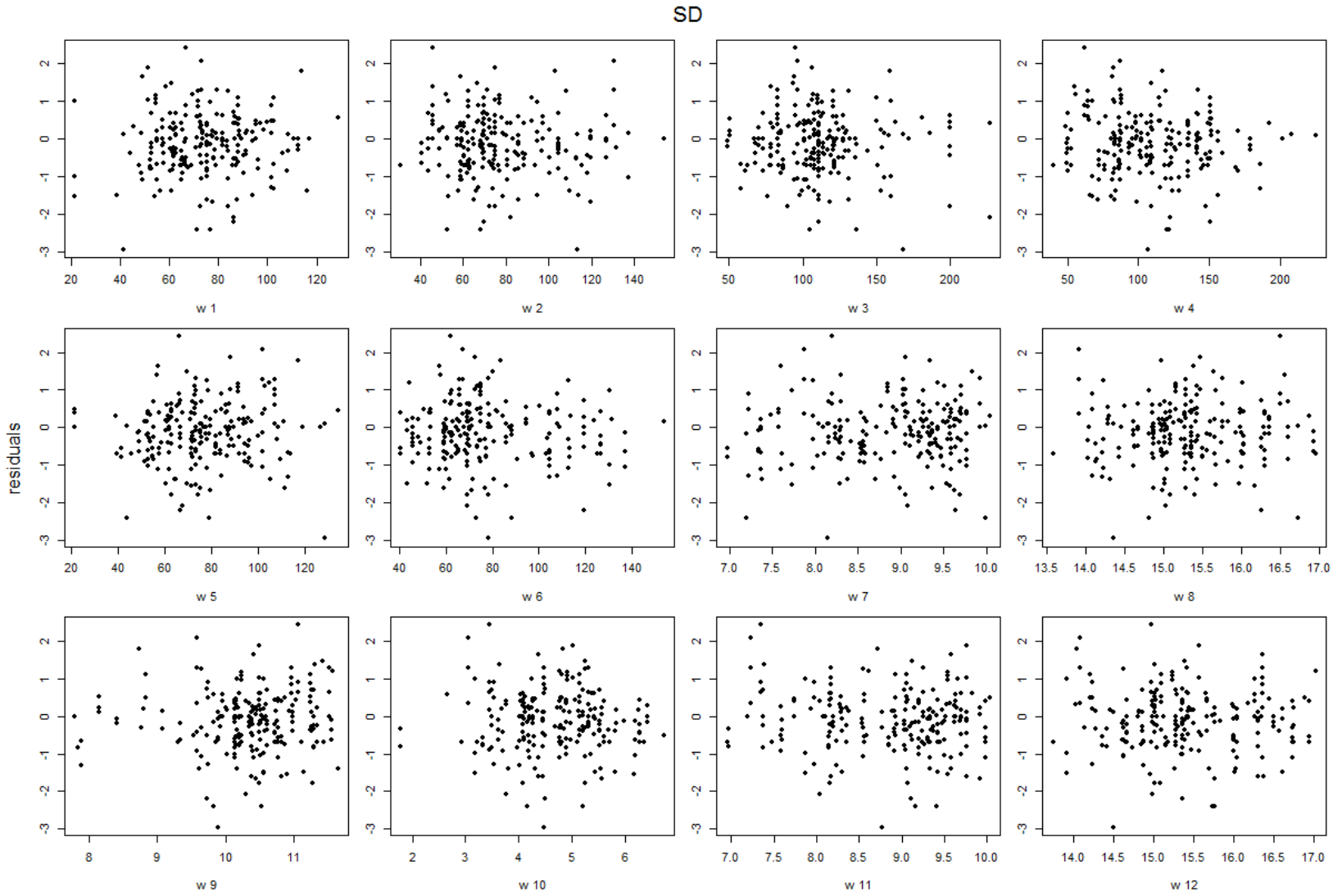
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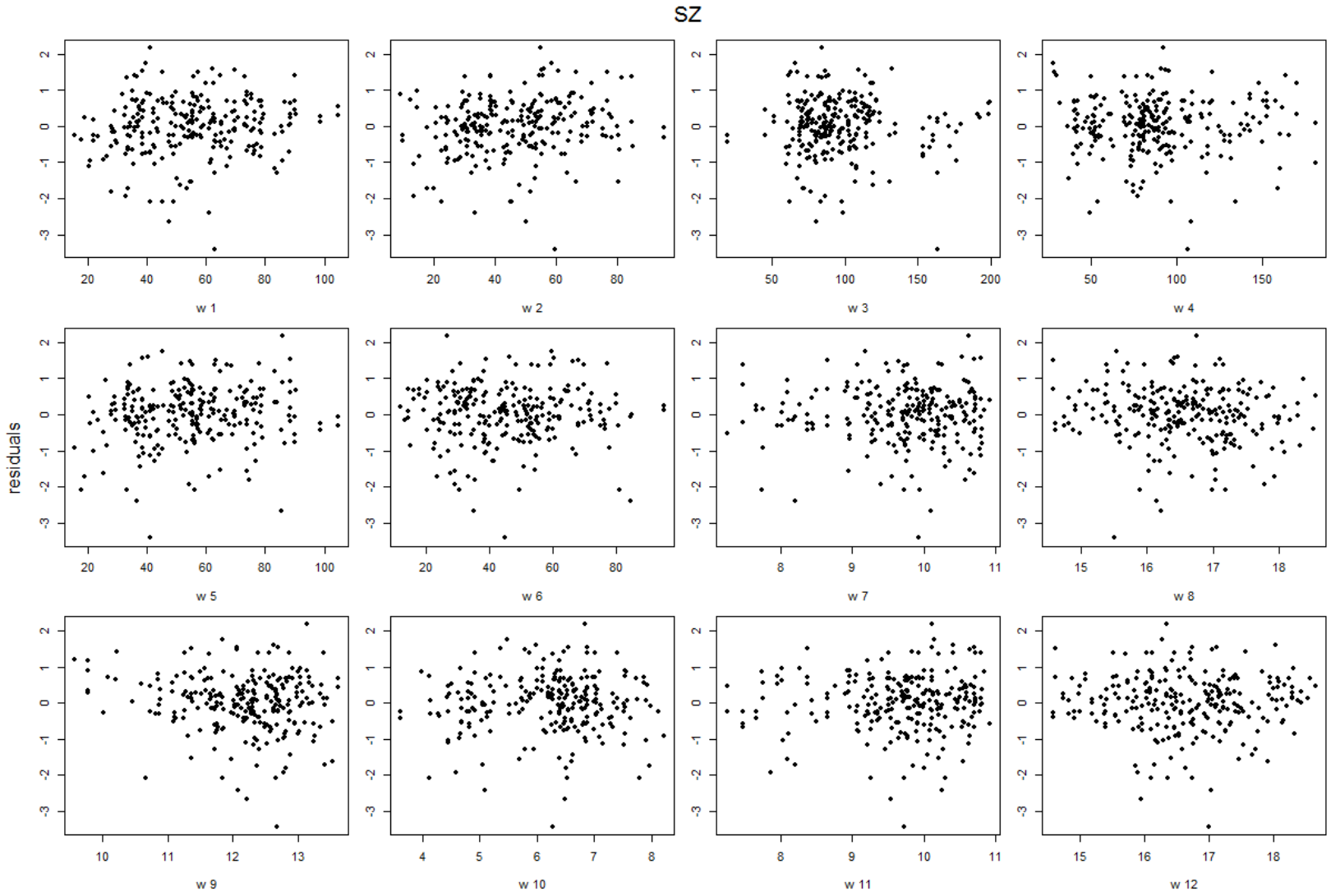
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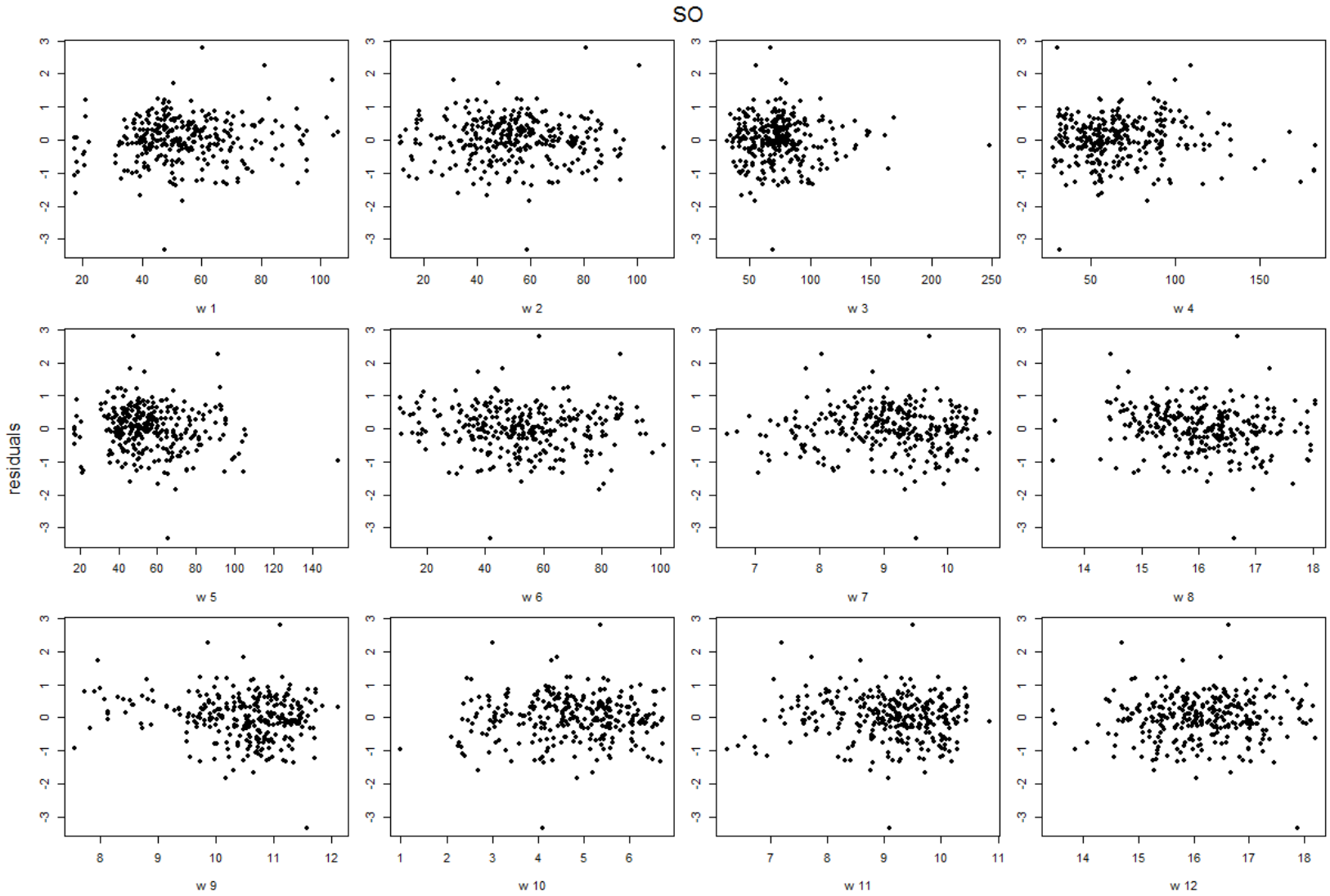
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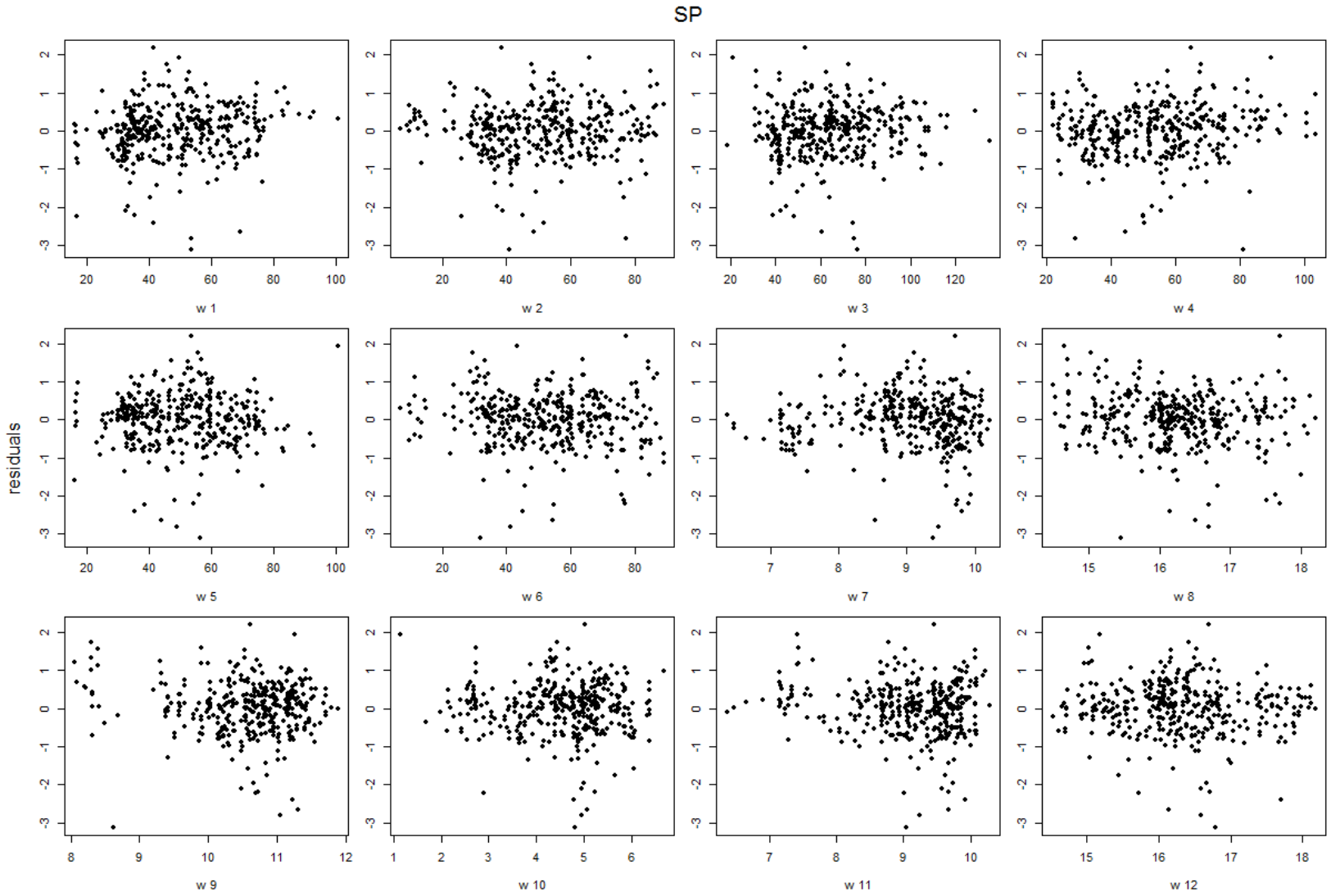
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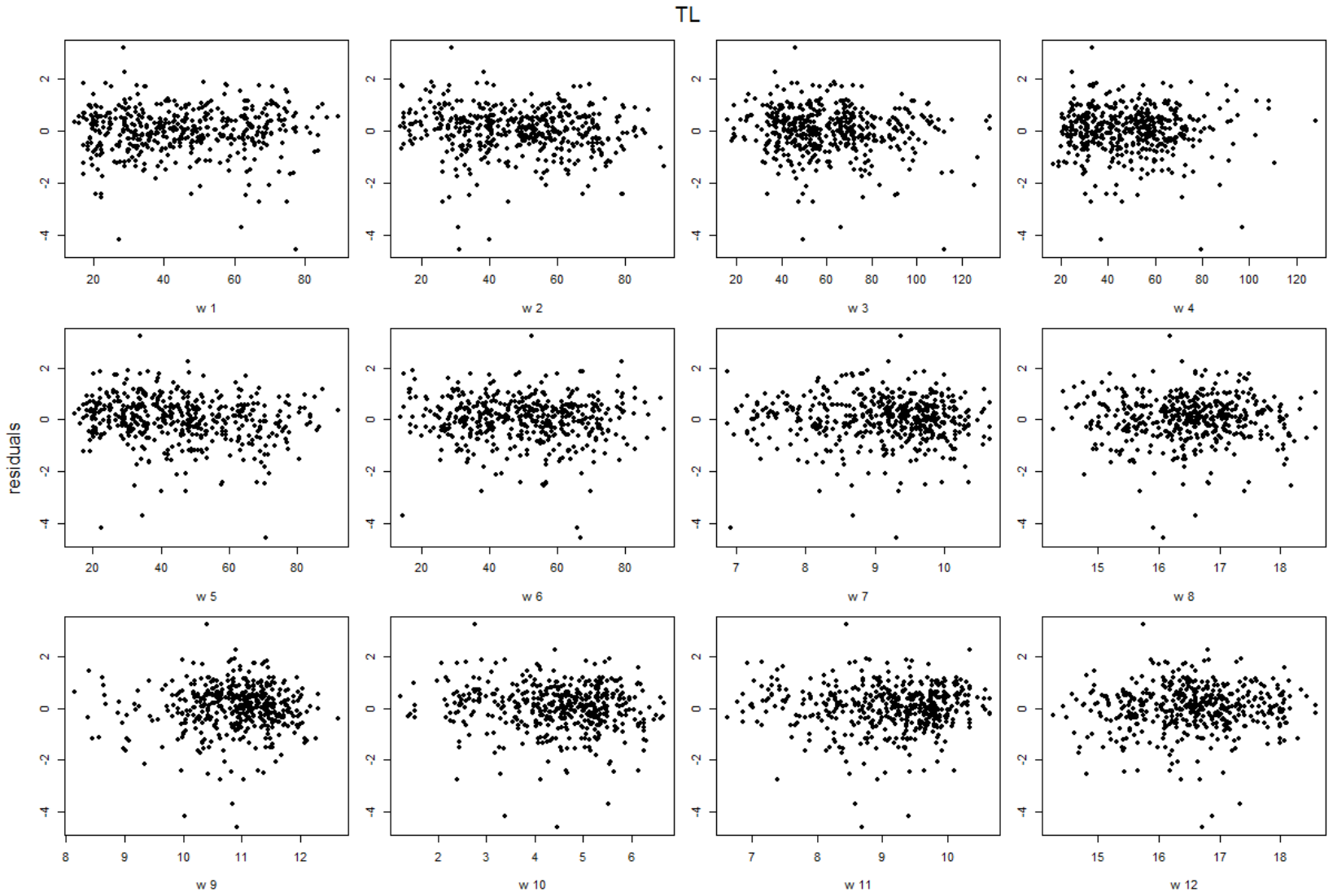
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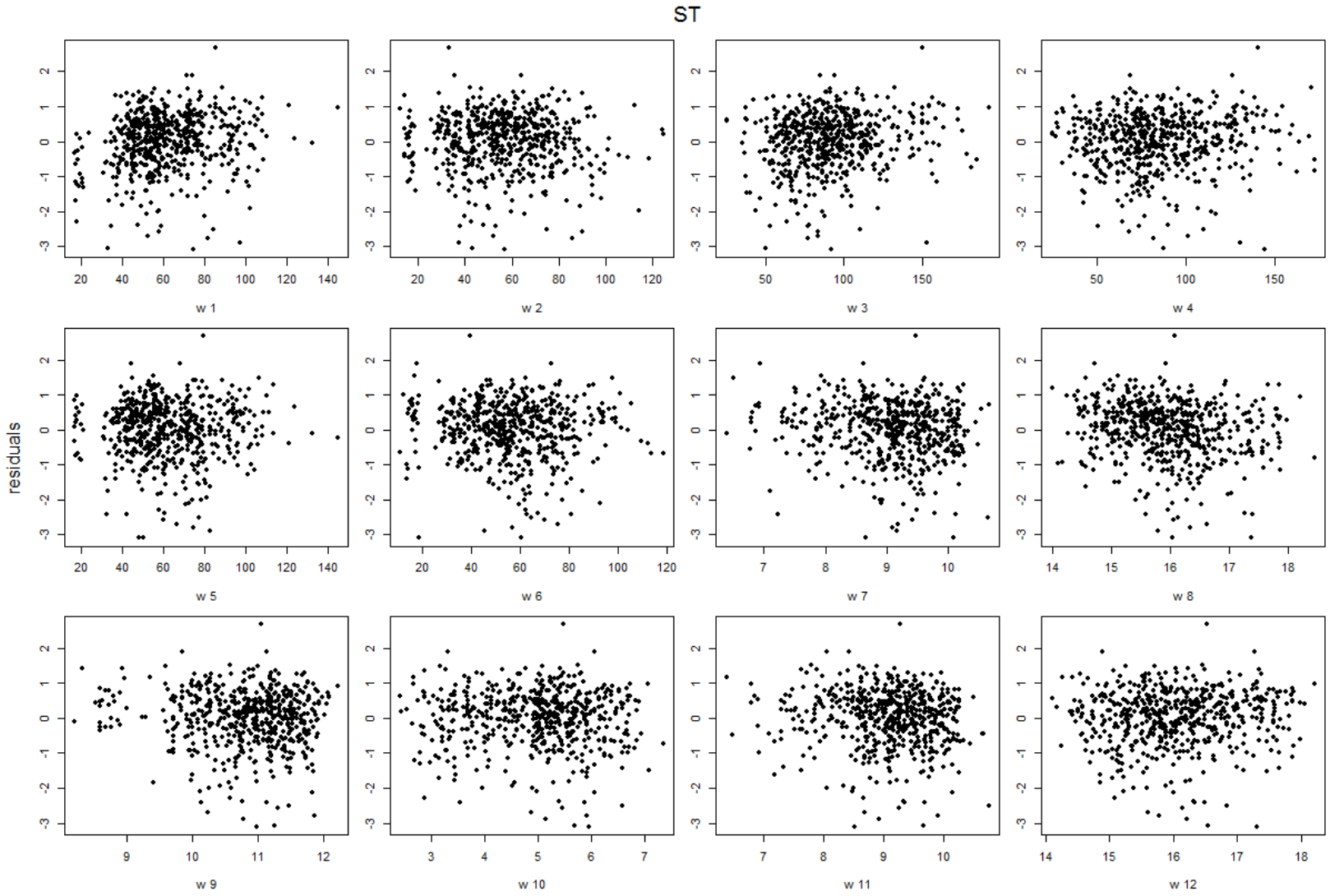
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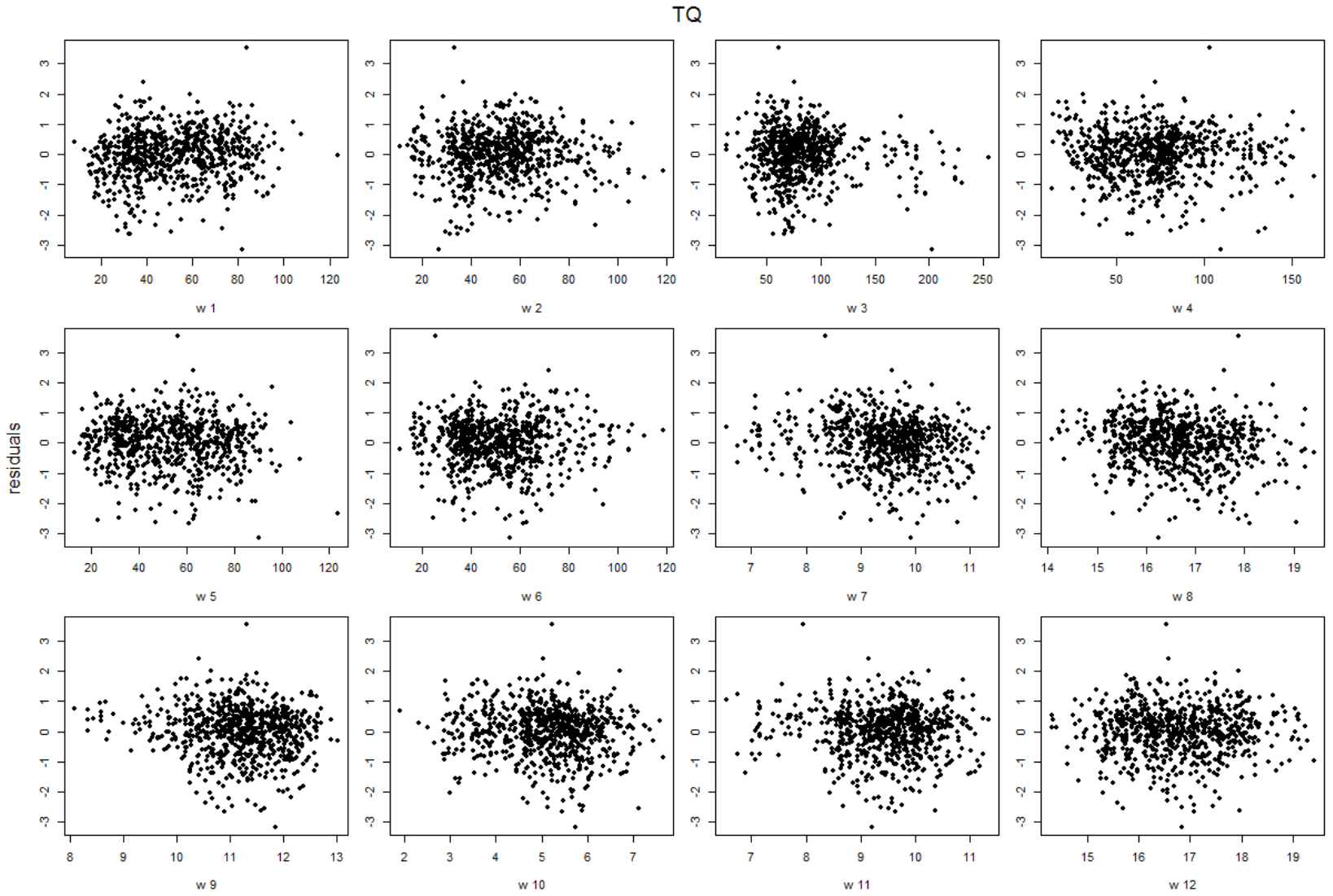
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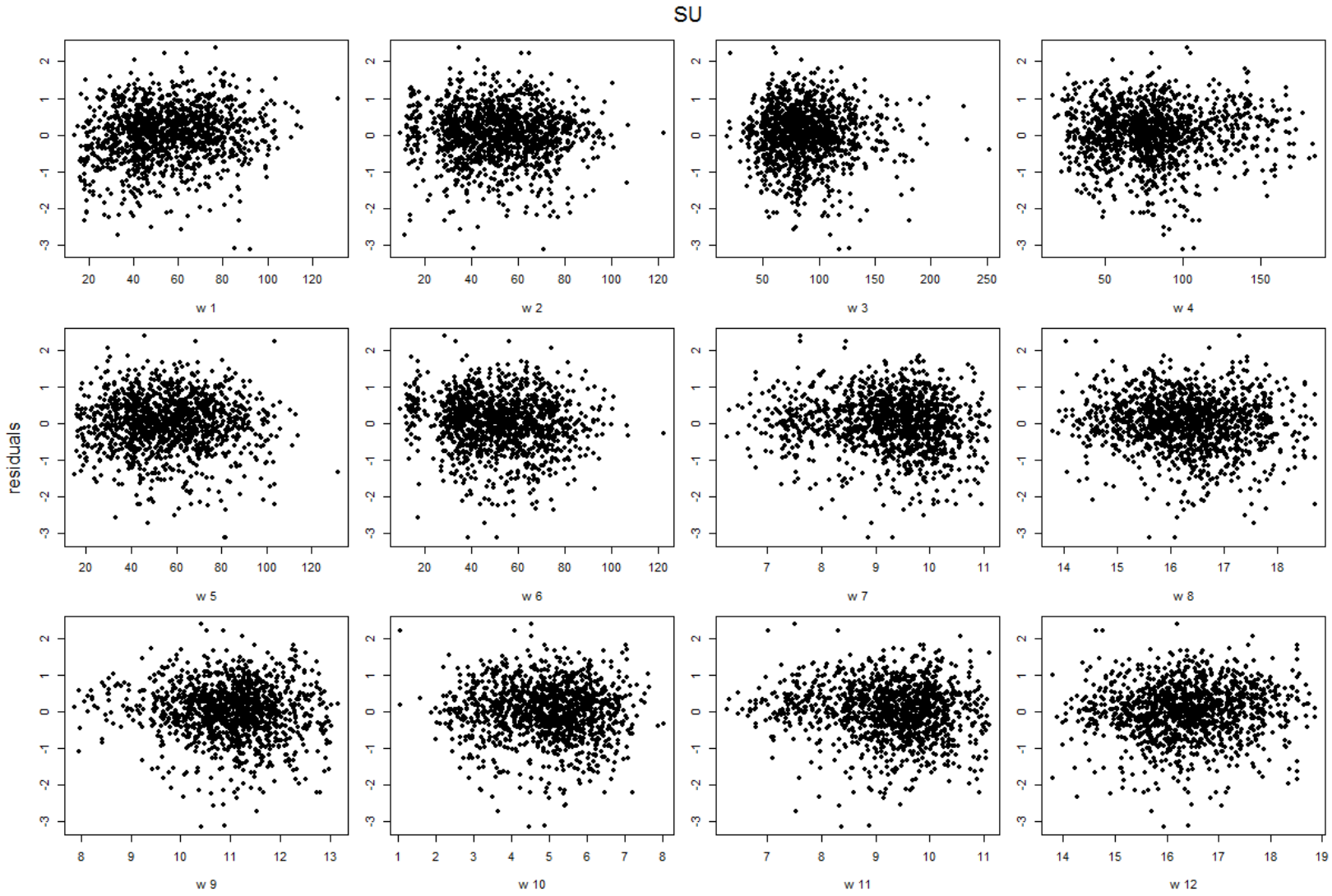
SU
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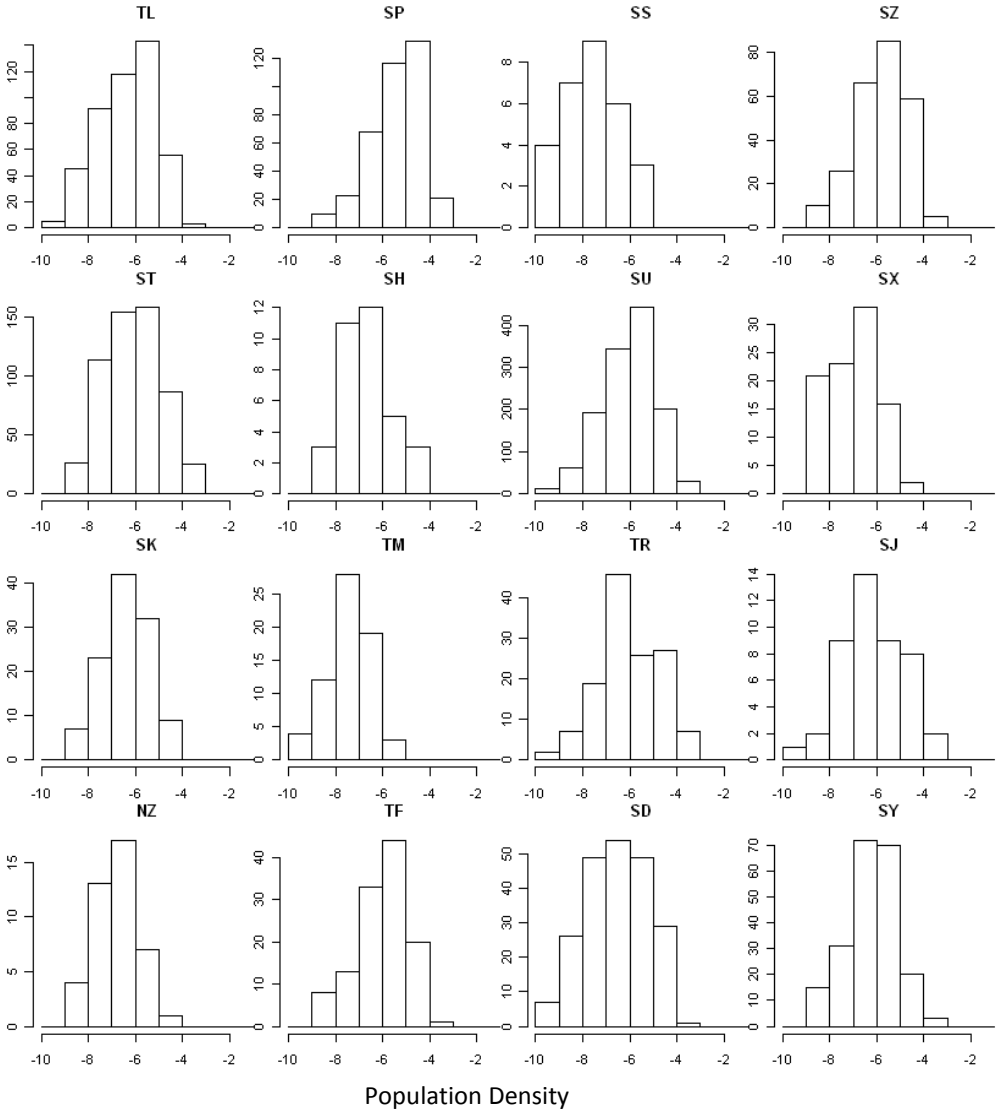
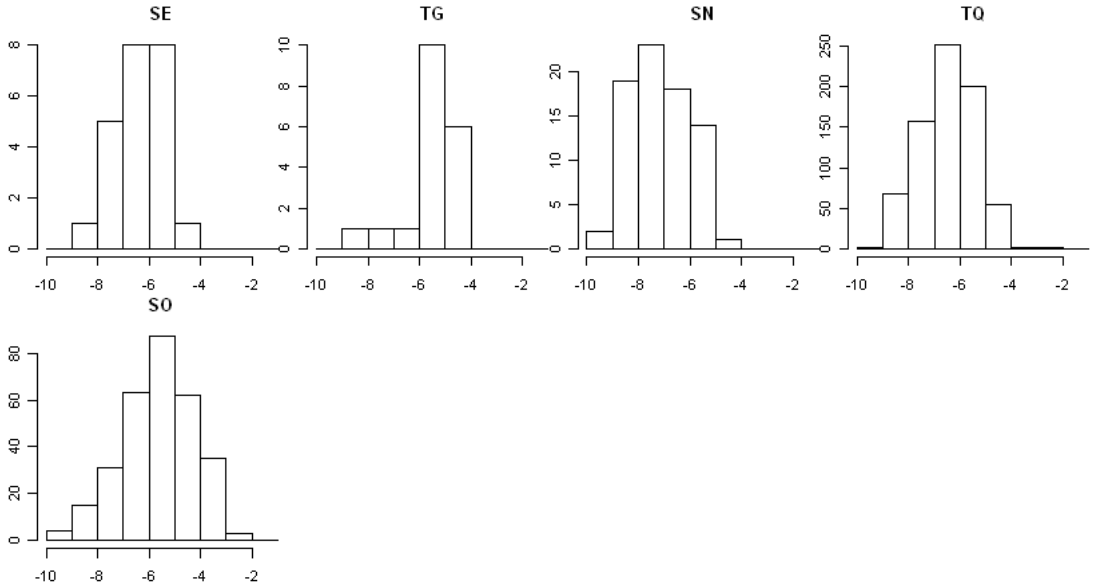
Fig. A.2. Histograms of regional large skipper log population densities (section 2.2.2.). At the top of each histogram is the region's OS grid reference.





Population Density

Appendix B

Table B.1. Candidate model statistics for the observation error model selection procedure when tested on a truncated simulated data set that included stochasticity and observation error but did not include Allee effects (section 3.3.3.). Italics indicate that the model converged between 20,000 and 200,000 iterations. NQ = negative quadratic density dependence. NL = negative linear density dependence. Null = no density dependence, i.e. the null model. Stoch = Stochasticity. Y_t is observed log per capita growth rate and x_t is observed unlogged population density.

	Data		
	No Allee, Stoch. + Obs. Error (N=25)		
Model	DIC	pD	dev
Including Error in Y_t^{obs} and x_t^{obs}			
NQ	*19.80*	*14.25*	*5.54*
NL	19.41	13.89	**5.52**
Null	21.46	12.91	8.55
Including Error in Y_t^{obs} and x_t^{obs}			
NQ	**10.57**	2.60	7.97
NL	10.78	2.56	8.216
Null	22.53	1.59	20.94

Appendix C

Table C.1. A shows the results for binomial regressions that tested how the detection of population-level Allee effects was affected by minimum population density for each species (section 4.2.1.). Significant results are indicated in bold. 'Total sites' is the total number of population with a distinct best model from the model selection procedure and 'Total Allee' is the number of those total populations for which an Allee effect was detected. *Euphydryas aurinia, Leptidea sinapis* and *Polymmatus coridon* had no populations exhibiting Allee effects and were therefore excluded from this analysis. B shows the species traits data used in the traits analysis in section 4.2.2. Mobility scores varied from 1 to 9 with 1 for species with the least movement and 9 for species with the most movement (Dennis 2010). Scores were derived using the following 9 variables: ex-habitat vagrants, garden records, urban central business district records, at-sea records, mass movements, range expansions, overseas migration from continent to Europe, regular reversed long distance migration, over-ocean (Atlantic) migration (Dennis 1993; Dennis 2005). Data for the three mate location sites, nectar plant (MLS nectar), host plant (MLS host) and physical edge (MLS phys edge), and the mate location method perching were obtained from Dennis 2010.

			A			B				
Species	Total sites	Total Allee	Estimate	Standard error	p value	Mobility	Perching	MLS nectar	MLS host	MLS phys edge
Aglais urticae	260	27	-488.49	492.50	0.32	8	1	0	1	1
Anthocharis cardamines	220	23	-2092.50	1103.24	0.06	5	0	1	1	1
Aphantopus hyperantus	155	7	-485.13	454.67	0.29	3	0	1	1	0
Argynnis aglaja	61	9	-1215.31	1283.52	0.34	5	0	1	1	0
Argynnis adippe	17	3	-8788.55	9013.92	0.33	3	0	0	1	1
Argynnis paphia	67	6	-789.28	788.09	0.32	6	1	0	1	1
Aricia agestis	100	14	-1142.06	1020.16	0.26	2	1	0	0	1
Boloria euphrosyne	26	2	-167.67	1140.19	0.88	2	0	1	1	0
Boloria selene	24	3	-586.36	1167.16	0.62	3	0	1	1	0
Callophrys rubi	87	4	-549.02	2041.37	0.79	3	1	0	0	1
Celastrina argiolus	154	15	-626.13	1186.83	0.60	6	1	0	1	1
Coenonympha pamphilus	142	13	-567.31	384.89	0.14	4	1	0	1	1
Cupido minimus	29	2	-432.68	1437.80	0.76	2	1	0	0	1
Erynnis tages	86	7	-1522.30	1202.29	0.21	2	1	0	0	1
Gonepteryx rhamni	205	14	-996.55	617.38	0.11	6	0	1	1	1
Hamearis lucina	23	3	-425.44	864.33	0.62	1	1	0	0	1
Hipparchia semele	41	4	-707.97	1155.70	0.54	3	1	0	0	1
Hesperia comma	21	1	-307.43	1263.69	0.81	2	1	1	0	1

Table C.1. continued.

			A			B				
Species	Total sites	Total Allee	Estimate	Standard error	p value	Mobility	Perching	MLS nectar	MLS host	MLS phys edge
Inachis io	227	10	-79.51	213.56	0.71	8	1	0	1	1
Lasiommata megera	90	7	-5275.93	3755.98	0.16	5	1	0	1	1
Limenitis camilla	**61**	**9**	**-14786.95**	**6336.96**	**0.02**	5	0	0	0	0
Lycaena phlaeas	204	22	-1945.74	1314.46	0.14	6	1	0	1	1
Maniola jurtina	170	4	-30.46	50.30	0.54	6	1	1	1	0
Melanargia galathea	136	11	-152.61	132.91	0.25	2	0	1	1	0
Neozephyrus quercus	56	9	-1536.61	2469.29	0.53	3	1	0	1	1
Ochlodes sylvanus	255	18	-1405.26	761.08	0.06	5	1	1	1	1
Pararge aegeria	**223**	**17**	**-1687.97**	**674.39**	**0.01**	Excluded from traits analysis (see page 81 for explanation)				
Pieris brassicae	**278**	**10**	**-2756.66**	**1306.26**	**0.03**	8	0	1	1	0
Pieris napi	**251**	**17**	**-1627.59**	**698.81**	**0.02**	7	0	1	1	1
Pieris rapae	249	7	-1057.22	773.82	0.17	8	0	1	1	0
Polygonia c-album	240	13	-522.67	784.96	0.51	6	1	0	1	1
Polyommatus bellargus	29	1	-73488.14	103274.38	0.48	1	0	1	1	0
Polyommatus icarus	218	9	-24.59	117.71	0.83	6	1	1	1	1
Pyrgus malvae	73	13	-1972.75	1471.19	0.18	2	1	0	0	1
Pyronia tithonus	188	6	-135.70	147.75	0.36	4	1	0	1	1

Table C.2. Results for binomial regressions that tested how the detection of population-level Allee effects was affected by minimum population density after elimination of the 'high densities only' populations of four species. (See main text for the criteria of 'high densities only' populations, section 4.2.1.). Significant results are indicated in bold. 'Total sites' is the total number of population with a distinct best model from the model selection procedure and 'Total Allee' is the number of those total populations for which an Allee effect was detected.

Species	Total sites	Total Allee	Estimate	Standard error	p value
Limenitis camilla	31	9	-5739.55	8580.13	0.504
Pararge aegeria	**172**	**17**	**-1672.90**	**686.19**	**0.015**
Pieris brassicae	191	10	-2210.90	1533.05	0.149
Pieris napi	188	17	-1390.40	798.32	0.082