



Striking the right balance between site and landscape-scale conservation actions for a woodland insect within a highly fragmented landscape: A landscape genetics perspective



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ABSTRACT

Landscape-scale conservation is increasingly seen as an effective strategy to combat habitat loss and fragmentation. However, there is debate on the relative merit and balance between site and landscape-scale conservation actions. Here, we provide much needed evidence to inform this debate. Our study, set in the highly fragmented landscape of the Isle of Wight, Southern England, focuses on the wood cricket (*Nemobius sylvestris*), a poorly dispersing woodland specialist. We use a landscape genetics approach, combining evidence from microsatellite DNA variation with an analysis of the contemporary landscape. Results revealed impacts of fragmentation in the form of high genetic differentiation and restricted gene flow between woodlands. Despite this, we found low relatedness, high genetic diversity and little evidence of inbreeding or bottlenecks. Our study also revealed that the present day landscape has only a limited role in explaining the observed genetic pattern. These results indicate that conservation actions for this study species should focus primarily on site-based activities to improve habitat quality and maintain large populations. However, we acknowledge that many other species that operate over larger spatial scales and have much smaller populations may be far more susceptible to habitat fragmentation and may benefit from wider landscape-scale actions. We demonstrate the utility and challenges of using landscape genetics to inform conservation strategies and we highlight the need to strike a balance between site and landscape-scale actions. Furthermore, our results suggest a blanket adoption of landscape-scale conservation strategies, no matter how appealing, may in practice be a poor use of conservation resources.

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1. Introduction

Many conservationists and policy makers now believe that landscape-scale conservation offers a more effective response to the increased threats from habitat loss and fragmentation than more traditional approaches based solely on the protection and management of individual biodiversity hot spots or sites (e.g. Worboys et al., 2010; Lawton et al., 2010). This approach is seen as especially important within highly fragmented and heavily modified landscapes, as these landscapes may compound the problem by impeding species movement and restricting gene flow (Storfer et al., 2010; Storfer et al., 2007). In general terms, fragmentation can reduce population sizes, reduce genetic diversity and increase the risk of local extinctions; while the increase in isolation can reduce the exchange of individuals and genes between fragmented populations (Fischer and Lindenmayer, 2007). Furthermore, it is also recognised that climate change may also exacerbate these threats as

species need to adapt to their new climate space (Oliver et al., 2012; Vos et al., 2008; Travis, 2003).

In an attempt to combat these impacts, landscape-scale conservation, often conceived as simply joining together apparently fragmented patches of habitat with corridors and stepping-stones, has been widely embraced by the conservation practitioner and policy communities (Lawton et al., 2010; Jongman and Pungetti, 2004; Opdam et al., 2006; Worboys et al., 2010). Although the concept of landscape-scale conservation is inherently appealing, logical and underpinned by sound scientific principles (e.g. Crooks and Sanjayan, 2006; Forman and Godron, 1986), support from empirical studies is currently both limited and equivocal (Humphrey et al., 2015; Eycott et al., 2012; Hodgson et al., 2009; Boitani et al., 2007; Bailey, 2007). As a result, there is currently much debate on the relative merit of, and balance between, site and landscape-scale conservation actions (e.g. Doerr et al., 2011; Hodgson et al., 2011; Oliver et al., 2012; Boitani et al., 2007). There is concern that this uncertainty is hindering the implementation of effective conservation strategies on the ground (Oliver et al., 2012; Boitani et al., 2007). There is therefore an urgent need to understand in which situation conservation would be best served by site-based actions to

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protect, manage and restore individual sites; as opposed to wider landscape-scale actions to create new habitat, establish corridors or stepping-stones between fragmented patches or actions to improve the matrix to enhance connectivity (Humphrey et al., 2015; Oliver et al., 2012; Lentini et al., 2013). In a time of limited resources, it is especially important to utilise sound scientific evidence to ensure that the right balance of conservation actions, particularly those involving expensive and ambitious landscape-scale actions, are directed towards those areas where they will produce the greatest biodiversity benefit.

The relatively new field of landscape genetics aims to address some of these fundamental conservation questions by combining the methods and ideas of population genetics with those of spatial landscape analysis to quantify the effect of landscape composition and configuration on genetic variation (Balkenhol et al., 2009a; Balkenhol et al., 2015; Storfer et al., 2007). The genetic data, based on molecular markers such as microsatellites or single nucleotide polymorphisms (SNPs), provide a snapshot of the accumulated effects of both historic and current processes on the pattern of genetic diversity observed within a study species. When combined with an analysis of the contemporary landscape it can provide important insights into the role of the landscape in determining important processes such as gene flow, connectivity and landscape permeability (Balkenhol et al., 2015; Storfer et al., 2010).

We illustrate the utility and application of this approach to inform conservation planning by applying it to the study of a woodland specialist species within a highly fragmented landscape and selecting robust and evidence-based conservation actions. The woodland specialist study species for this study is the wood cricket (*Nemobius sylvestris* (Bosc D'Antic 1792)) (Orthoptera: Gryllidae). Wood crickets occur across Europe and North Africa and the sites in England represent the most north-western extreme of their distribution (Harz, 1969). Previous studies (Brouwers and Newton, 2009) revealed that wood crickets have specialist habitat requirements, occupying areas of open broadleaf woodland habitat where they are often locally abundant. They are a flightless, ground-moving species with limited movement potential and are apparently reluctant to move through non-wooded habitats. In support of their limited movement, Brouwers and Newton (2009) found that the presence of wood crickets in woodlands was negatively correlated with the distance to the nearest occupied woodland. In 2005 an extensive survey of 147 suitable woodland fragments by Brouwers and Newton (2009) found that only 32 woodlands (20%) were actually occupied by wood crickets, even though many appeared to have suitable habitat conditions. Most occupied sites consisted of those larger woodlands that were relatively close (<50 m) to other occupied woodlands. This confirms that wood crickets are a potentially fragmentation sensitive, woodland specialist species which may be suffering from woodland fragmentation and may benefit from a landscape-scale conservation strategy.

This study uses a landscape genetics approach to answer the following questions to inform the prioritisation of site versus landscape-scale conservation actions for the selected study species within fragmented landscapes: (i) Is there evidence for fragmentation and isolation effects on the study species, with respect to genetic differentiation and restricted gene flow between populations? (ii) If there is evidence of fragmentation, is there evidence that it may be causing long-term adverse impacts for the species populations, in terms of high relatedness, low genetic diversity, signs of inbreeding or recent genetic bottlenecks? (iii) If there is evidence of gene flow between fragmented populations, do particular contemporary landscape features help to explain this pattern?

2. Methods

2.1. Study landscape

The Isle of Wight (IoW), located 10 km off the south coast of England, was selected as the highly fragmented landscape. The island

covers an area of 380 km² and has a human population of approximately 125,000. It has been separated from mainland England for around 6000 years (Basford, 2008). The long land-use history of the island, in common with many agriculturally dominated landscapes throughout the world, has resulted in a highly modified landscape interspersed with small, scattered fragments of broadleaf woodland (Quine and Watts, 2009). Today, the IoW landscape consists of 66% agricultural land, 12% urban/residential and 12% woodland of which only 2% is classed as ancient semi-natural woodland (i.e. determined to have been present since at least 1600 AD) (Anon, 2002; Basford, 2008). However, the remaining woodland fragments retain considerable conservation value with many species dependent on their continued existence for survival (Pope et al., 2003).

Wood crickets were first recorded on the IoW in the 1890s (Morey, 1909) and are considered to be native to the island. Apart from the IoW, the stronghold of wood crickets in southern England is in the New Forest, they occupy very few other sites elsewhere in the south of England (NBN Gateway, <http://data.nbn.org.uk/> accessed June 2015).

2.2. Data collection

In the summer of 2007, a total of 943 wood crickets were sampled (Fig. 1, Table 1) from 12 individual woodlands on the IoW (Brouwers and Newton, 2009). Three pairs of woodlands (woodlands (1 & 2), (6 & 7) and (9 & 10)) were virtually adjacent to each other (Fig. 1). An additional 83 individuals were collected from two woodland sites on the English mainland, to act as out groups and reference sites. One mainland sampling site was in the New Forest (woodland 14), which contains the largest population of wood crickets in England, and the other was a more distant site in Offwell, Devon (woodland 13). The larger woodlands on the IoW seemed to contain several discrete populations of crickets, as a result crickets were collected from a total of 34 sample groups within the 12 woodlands (Fig. 1, Table 1). For some analyses these 34 sample groups were reduced to 23 due to the application of the additional criterion that a group had to contain at least 20 individuals.

Sampled crickets were stored in 100% ethanol at -20°C . One hind leg per cricket was air dried for 15 min prior to DNA extraction using the high salt method (Sunnucks and Hales, 1996). DNA yield was measured using a spectrophotometer (Eppendorf) and extracts were diluted to 5 pmol/ μl for PCR. Fourteen microsatellite loci (Supplementary Table S1) developed specifically for *N. sylvestris* were amplified using the primer pair sequences and PCR conditions described by Vanhala and Cottrell (2008). An additional locus was also developed by these authors, NSD012 (GenBank accession number HM143920). PCR products were run on a LI-COR 4300 sequencer (LI-COR Biosciences) and alleles were scored manually using ladders of known molecular weight as standards.

All samples were amplified with 10 markers. The utility of using the remaining five markers (NSA004, NSA006, NSD102, NSD133, and NSD137) to clarify the genetic structure further was explored in a sub-sample of the data but they did not change the results based on the 10 markers (See Supplementary Table S1 for detailed information on markers and sample numbers). The data were checked for errors and null alleles using Micro Checker (Van Oosterhout et al., 2004). Deviations from Hardy–Weinberg equilibrium (HWE) were estimated using Genepop v. 4 (Rousset, 2008). Deviations from linkage equilibrium (LE) were estimated with FSTAT v. 2.9.3.2 (Goudet, 2013) using the log likelihood ratio test statistic and 2100 permutations (p-value for 0.05 level was 0.000476 after Bonferroni correction).

2.3. Genetic differentiation and restricted gene flow

Evidence of fragmentation in terms of genetic differentiation and structure between populations within the 14 sampled woodlands was investigated with the program STRUCTURE v.2.3.4 (Falush et al., 2007; Hubisz et al., 2009; Pritchard et al., 2000). Woodland 13, on the English

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