ORIGINAL CONTRIBUTION

Inter-individual variation in colour patterns in noctuid moths characterizes long-distance dispersers and agricultural pests

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Abstract

A high capacity for long-distance dispersal is a key to success for species confronted with environmental heterogeneity, habitat modification, fragmentation and loss. However, dispersal capacity is difficult to quantify and therefore poorly known in most taxa. Here, we report on a test for an association of variation in dispersal capacity with variable colouration of noctuid moths. First, using data from 12 experienced lepidopterologists, we showed that despite variation among experts in average assessments, different species are consistently classified as having non-variable, variable or highly variable colour patterns when assessed by different experts. We then compared the incidence of non-resident species with high inter-individual variation in colour patterns recorded on the isolated island Utklippan ($n = 47$), with that in a species pool of potential long-distance dispersers from the nearest mainland ($n = 295$). Species with high inter-individual colour pattern variation were over-represented on the island compared with species having non-variable colouration. This finding constitutes rare evidence from the wild of long-distance dispersal, measured on a spatial scale relevant for moths when tracking habitats in fragmented and changing landscapes or when keeping pace with environmental challenges associated with climate change. Finally, we showed that Swedish noctuid moths classified as agricultural pests ($n = 28$) had more variable colour patterns compared with non-pests ($n = 368$). The majority of agricultural pests were also recorded on the isolated island, an outcome that is indicative of pest species having high dispersal capacity. Data on colour pattern variation may thus offer a simple and cost-effective proxy to estimate dispersal capacity and can also help identify potential pest species. Our findings are potentially useful when modelling and predicting population and range dynamics of species in spatiotemporally heterogeneous environments, with direct implications for conservation biology and pest management.

KEYWORDS
colour pattern variation, expert evaluation, Lepidoptera, mobility, Noctuidae, trait

1 | INTRODUCTION

The ability to disperse and move through the landscape is an important feature of species' ecology. Virtually, all species are confronted with challenges associated with spatial and temporal environmental heterogeneity, and a high capacity for long-distance dispersal is a key to success in finding new areas, suitable for survival and reproduction. Knowledge of dispersal capacity and movements is required to better understand, model and

predict population dynamics and distribution shifts of species in fragmented and temporally changing landscapes, with direct implications for the design of conservation efforts and also for management actions aimed at agricultural pests and invasive species. However, dispersal capacity is poorly known in most taxa (Burke, Fitzsimmons, & Kerr, 2011) due to difficulties in collecting, measuring or categorizing species characteristics related to dispersal (Murray, Rosauer, McCallum, & Skerratt, 2011; Stinner, Barfield, Stimac, & Dohse, 1983). This is specifically true in many insects, constituting the vast majority of the invertebrate fauna.

In insects, mark–release–recapture experiments, laboratory tethered flight experiments, experimental releases in the field and expert evaluations have been used to estimate dispersal capacity (Burke et al., 2011; Jones, Lim, Bell, Hill, & Chapman, 2016; Kuussaari, Saarinen, Korpela, Pöyry, & Hyvönen, 2014; Nathan et al., 2008; Novotný, Zapletal, Kepka, Beneš, & Konvička, 2014; Stevens, Turlure, & Baguette, 2010; Summerville, Conoan, & Steichen, 2006). These approaches usually include a restricted number of species, are performed as laboratory experiments, at spatial scales involving local movements, or depend on the accuracy in the expert evaluation of species' dispersal capacity. Therefore, to develop suitable methods for multispecies comparisons of dispersal capacity at larger spatial scales in the wild, for applications in ecology and conservation of biodiversity, is a great challenge. Another field of great importance is to better understand population dynamics of agricultural pest species and outbreak dynamics (Battisti & Larsson, 2015). One challenge associated with forecasting pest impacts in agricultural landscapes is to link key traits with variables of importance for dispersal, population growth, dynamics and persistence (Ovaskainen et al., 2019; Terblanche, Karsten, Mitchell, Barton, & Gilbert, 2015).

One way to identify proxies for dispersal capacity is to use indirect estimates based on traits that are thought, or proven, to be associated with differences in dispersal capacity. Earlier studies have indicated a number of species traits and ecological characteristics as related to dispersal capacity in a wide range of organisms, such as hind-foot length in voles (Forsman, Merilä, & Ebenhard, 2011; Shine, Brown, & Phillips, 2011), wing length in birds and insects (Berggren, Tinnert, & Forsman, 2012; Rundle, Bilton, Abbott, & Foggo, 2007; Sekar, 2012; Stevens et al., 2010), and body size in eels (Forsman & Berggren, 2017).

Another candidate trait in this respect is inter-individual variation in colour patterns. In moths, previous studies have shown that high inter-individual colour variation is related to higher average abundances and dampened population fluctuations (Forsman, Betzholtz, & Franzén, 2015), faster poleward range shifts (Forsman, Betzholtz, & Franzén, 2016), lower extinction risk (Betzholtz, Franzén, & Forsman, 2017) and larger continental range sizes (Franzén, Betzholtz, & Forsman, 2019). To our knowledge, it has not previously been investigated if more variable colour patterns in moths are associated with greater dispersal capacity, or whether colour pattern variation is greater in pest as opposed to non-pest species.

Here, we explore whether inter-individual variation in colour patterns may be used as proxy for dispersal capacity in noctuid moths, and whether colour patterns are more variable in agricultural pests than in non-pests. We first evaluate inter-rater reliability of expert classifications of variation in colour pattern, that is, the extent to which different researchers are consistent in their assessment of colour pattern variation, and, conversely, the extent to which different species are consistently classified as non-variable, variable or highly variable by different experts. We further aim to obtain a quantitative measure of the inter-individual variation in colour pattern within species using a higher resolution continuous scale that opens for alternative statistical approaches. Additionally, we examine the agreement between the continuously distributed measure of colour pattern variation, as calculated across several independent experts, and the three discrete categories (non-variable, variable, and highly variable) used in previous studies. Thereafter, we evaluate whether colour pattern variation is associated with dispersal capacity and control for other traits of possible importance: host plant specificity, habitat specificity, size and length of the flight period. To this end, we compare the incidence of variable colour patterns among non-resident species of moths captured on an isolated island with that in a sample of species on the nearest mainland that comprise the pool of potential long-distance dispersers. Lastly, we investigate whether moth species that are generally regarded as agricultural pests have more variable colour patterns, and whether they are also recorded on the isolated island, outcomes both of which would be indicative of pest species having a high dispersal capacity.

2 | MATERIALS AND METHODS

2.1 | Study area and design

The study area consists of the outpost island Utklippan and the province of Blekinge, southeast Sweden (Figure 1). Utklippan (9 ha) is situated 16 km from mainland Blekinge, is made up of primary rocks, with just a few plant and tree species. The sparse vegetation is characterized by adaptations to abiotic factors such as windy conditions and salt spray. As a result, very few moth species reproduce on the island. The province Blekinge (29.000 km^2) contains the most important habitat types of southern Sweden: semi-natural grasslands, arable fields, deciduous and conifer forests. We recorded night-active moths on Utklippan by operating an automatic light-trap (125 W UV bulb) during May through October in 2004–2006. We focused on the family Noctuidae (Aarvik et al., 2017) because they show a similar degree of attraction to UV light sources (Scoble, 1988). For the purpose of this study, those species that were captured on the island were considered as having a higher capacity for long-distance dispersal, compared with species that were present on the mainland but not recorded on the island. Thus, the province of Blekinge was defined as the potential species pool of migrants to the island Utklippan (n = 295). Even though there is a possibility that some individuals recorded on Utklippan actually travelled longer distances,
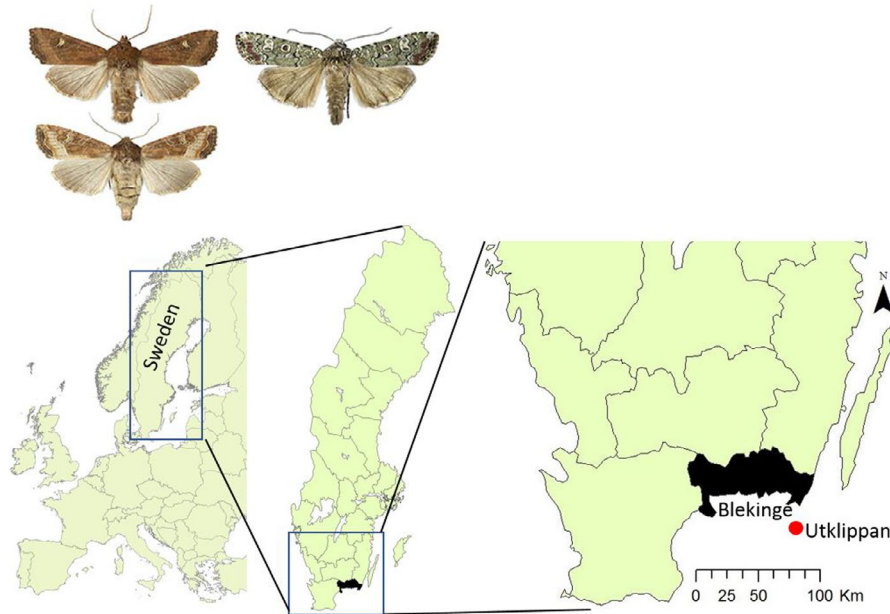
FIGURE 1 Map of the study area. To evaluate the relation between colour pattern variation (CPV) and long-distance dispersal, we used species recorded on the isolated island Utklippan and the nearest mainland Blekinge as the pool of potential dispersers. The island Utklippan is indicated by a red dot, and mainland Blekinge is indicated in black. To evaluate the association between CPV and agricultural pest status, we used noctuid moths recorded from all of Sweden. Photographs of noctuid moths representing species with variable (*Calaena leucostigma*, left) and non-variable (*Actebia praecox*, right) colour pattern variation. The score for those species in the expert classification was 0.79 and 0.13, respectively (see Methods for details). Photographs by Vladimir S. Kononenko [Colour figure can be viewed at wileyonlinelibrary.com]

the noctuid moth fauna of other areas around the Baltic Sea is quite similar to the one in Blekinge (Karsholt & Nielsen, 1998).

One of the main aims of this study was to explore long-distance dispersal in noctuid moths. Therefore, we excluded species that we categorized as resident (i.e., reproducing) on the island Utklippan from the analysis. A resident species meets three criteria: recorded on the island at least 2 of the 3 years in the study, the preferred habitat(s) occur(s) on the island and the larval host plant is growing on the island (Mattsson, 1976; Widgren, 1999). This procedure identified 48 species as resident on the island. These species were thus excluded from the analysis, leaving 247 noctuid species in the pool of potential dispersers from mainland Blekinge.

2.2 | Expert evaluation of colour pattern variation

Inter-individual variation in colour pattern of all noctuid moth species included in the study was assessed independently by 12 Swedish lepidopterologists as non-variable (0), variable (1), or highly variable (2) (details in Appendix S1 and S2). To obtain a continuous measure of colour pattern variability for each species, a mean value of colour pattern variation was calculated for each species across the values assigned by the twelve independent experts. The mean values were then divided by 2 (the highest possible value) to generate an expert score with a continuous distribution that ranges from 0 to 1 (Appendix S3). Photographs of noctuid moths with low and high expert score of colour pattern variation are available in Figure 1.

In previous investigations into the consequences of inter-individual variation in colour patterns in moths (Betzholtz et al., 2017;

Forsman et al., 2015, 2016; Franzén et al., 2019), we have relied on a discrete classification with three categories: non-variable; variable; or highly variable colour patterns. These expert classifications have been performed by two of the authors (MF & PEB), as described in previous contributions. Here, we also set out to evaluate the inter-rater reliability of expert classifications of variation in colour pattern, that is, the extent to which different researchers are consistent in their assessment of colour pattern variation (see Appendix S1).

2.3 | Species traits

In the analysis used to test for an association of variable colour pattern with long-distance dispersal and with being an agricultural pest species, we also evaluated the roles of four other traits that may contribute to variation in dispersal capacity and pest status among species of noctuid moths (Betzholtz & Franzén, 2011, 2013): host plant specificity, habitat specificity, size, and length of the flight period. We categorized host plant specificity in relation to the number of larval host plants species according to Emmet (1991), Huldén, Albrecht, Itämies, Malinen, and Wettenhovi (2000) and Svensson (1993); monophagy when larvae feed on a single species only, oligophagy when larvae feed on a maximum number of five plant species (restricted to one genus/family) and polyphagy when larvae feed on more than six plant species (from two or more genera/families). We categorized habitat specificity broadly in four different categories according to Emmet (1991), Huldén et al. (2000) and Skou (1991): deciduous forest, coniferous forest, open habitats (grasslands and other open areas) and habitat generalists. We quantified

TABLE 1 The best-fitting generalized mixed linear model (AIC = 336.2) explaining a high capacity of long-distance dispersal in non-resident noctuid moths on the island Utklippan (*n* = 47), compared with a species pool of potential dispersers from the Swedish mainland (*n* = 247). Null model had AIC = 355.3

Variable	Estimate	Std. Error	z-value	P
Colour pattern variation	0.779	0.3434	2.27	0.0233
Length of adult flight period	0.260	0.0732	3.54	0.0004

size using the male wingspan (mm), as a continuous variable, according to Emmet (1991) and Skou (1991). Finally, we quantified length of adult flight period in weeks, as a continuous variable, according to Svensson (1993). In species where two annual generations occur, we summed the flight periods.

2.4 | Statistical analyses

We used a generalized mixed linear model (GLMM) with binomial error distribution and a logit link function to evaluate whether the incidence of variable colour pattern (lognormal) was higher among species recorded, but not reproducing, on the island than in the sample of species from the nearest mainland. In this approach, a positive outcome would be interpreted as evidence that species having more variable colour patterns also have a higher capacity for long-distance dispersal. However, we also consider alternative interpretations in the discussion section. In the analysis, we controlled for four additional traits that have earlier been suggested to potentially influence dispersal capacity in moths (Betzholtz & Franzén, 2011, 2013): host plant specificity, habitat specificity, size and length of the flight period. We tested for effects on dispersal capacity of variable colour pattern and the four additional explanatory variables. We also included effects of all possible two-way interactions of colour pattern variation and the other four traits. We then selected the best model according to the Akaike information criterion (AIC; Burnham & Anderson, 2002). Genus was included as a random factor in the models to partially account for greater similarity among more closely related species (Forsman et al., 2015, 2016).

The data set used to evaluate the role of variable colour pattern for agricultural pests consists of all noctuid moth species recorded in Sweden (*n* = 396). Among those, there are 28 species that have been previously identified as agricultural pests in other sources (AGRIS, 2016; Ahola & Silvonen, 2005, 2008, 2011; Alford, 2017) (Appendix S3). We used the same statistical approach, a GLMM model as described above, to evaluate whether the incidence of variable colour pattern (lognormal) was higher among species categorized as agricultural pests than as non-pest species. Also here, we included genus as a random factor, but we did not consider the possible role of interactions between explanatory variables and colour pattern variation. The number of pest species was small (*n* = 28) and

including interactions would have resulted in over-parameterization. To further evaluate the role of long-distance dispersal capacity in agricultural pests, we used the set-up described above for evaluating long-distance dispersal per se, with mainland Blekinge as the species pool of potential migrants to the isolated island Utklippan. In this dataset, we included 21 agricultural noctuid moths because seven of the agricultural pest species have not been recorded in Blekinge.

All analyses (except those reported in Appendix S1) were conducted in the R software environment 3.5.1 (R Development Core Team, 2018) and the lme4 package (Bates & Maechler, 2010). We used the method described in Nakagawa and Schielzeth (2013) to obtain values for the explained variance in the final GLMM.

3 | RESULTS

Expert classifications of inter-individual variation in colour patterns of moths showed that there were differences among scorers in how they judged the average level of colour pattern variation. Despite the variation among scorers, different species were consistently classified as non-variable, variable or highly variable by independent experts, and there were significant differences in average colour pattern variation among the different moth species (Appendix S1, Figure S1). The original classifications of colour pattern variation into three categorical levels could be converted into a mean colour pattern variation score with a continuous frequency distribution (Appendix S1, Figure S1). The continuously distributed measure of colour pattern variation was closely related with the three discrete categories (non-variable, variable, and highly variable) that have been used in previous studies (Appendix S1, Figure S2).

On the island Utklippan, we recorded 95 out of the 295 noctuid moth species from the species pool of potential migrants on the Swedish mainland. Of these, 47 species were non-resident on the island, hence categorized as having high dispersal capacity. The best model (according to AIC) showed that colour pattern variation and length of adult flight period was significantly related to a high capacity of long-distance dispersal in non-resident noctuid moths on the island Utklippan (Table 1, *p* = 0.023, *p* < 0.001, respectively). None of the other three traits that we controlled for in the analysis, or any of the two-way interaction terms between colour pattern variation and the other traits, were related to long-distance dispersal. The final best model (AIC = 336.2, Table 1) provided a better representation of the variation in the data compared to the null model only including the random structure (AIC = 355.3). The capacity for long-distance dispersal increased with increasing colour pattern variation (odds ratio 2.18 [95% CI: 1.11–15.47]) and with increasing length of the flight period (odds ratio 1.30 [95% CI: 1.12–9.20]). The proportion of variance explained by the fixed factor alone was 11% and the proportion of variance explained by the fixed and random factors together was 44%.

Moth species previously categorized by other researchers as agricultural pests had more variable colour patterns compared to non-pests. The best model (according to AIC) showed that colour

pattern variation and length of the adult flight period was significantly related to pest status (Table 2, $p = 0.006$, $p < 0.001$, respectively). The final best model (AIC = 150.8, Table 2) provided a better representation of the variation in the data than the null model only including the random structure (AIC = 179.3). Finally, 76% (16 out of 21) of the pest species in the pool of potential dispersers from mainland Blekinge were recorded on the isolated island Utklippan, also supporting the notion that agricultural noctuid pests have a high capacity for long-distance dispersal.

4 | DISCUSSION

Here, we present the first evidence that differences in colour pattern variation among species of noctuid moths can be assessed with high reliability by independent expert lepidopterologists. Another major conclusion emanating from this study was that colour pattern variation in moths may be used as a multispecies proxy for dispersal capacity at larger spatial scales. Results indicate that species with high inter-individual colour pattern variation have higher dispersal capacity than do species that do not vary in their colouration. Because data on colour pattern variation is relatively easy to extract for many taxa this could be an attractive possibility, for example when predicting range dynamics in fragmented and changing landscapes and when conservation measures of species and habitats are devised. The spatial scale of the present study strengthens the inference space of the results, because our findings are based on distances relevant for noctuid moths when tracking resources and habitats in fragmented and changing landscapes, or when keeping pace with a changing climate (Betzholtz, Petersson, Ryrholm, & Franzén, 2013; DeVictor et al., 2012; Forsman et al., 2016; Loarie et al., 2009). Further, we also indicated that variation in colour patterns is greater in agricultural noctuid pests than in non-pest species. This effect remained also when other traits that might be associated with high capacity for dispersal, range expansions and potential for rapid population growth were statistically taken into consideration. The association of colour

TABLE 2 The best-fitting generalized mixed linear model (AIC = 150.8) explaining the importance of traits in agricultural noctuid pests in Sweden ($n = 28$), compared with non-pest species ($n = 368$). Null model had AIC = 179.3

Variable	Estimate	Std. Error	z-value	P
Colour pattern variation	2.311	0.8323	2.78	0.0055
Length of adult flight period	0.290	0.0674	4.30	<0.001
Host plant specificity	1.557	0.9480	1.64	0.1007
Habitat specificity	18.67	4703.1	0.01	0.9968
Size	0.047	0.0325	1.45	0.1472

pattern variation and other key traits, such as host plant and habitat specificity, size and length of flight period could therefore contribute to better understanding of population dynamics and pest management (Battisti & Larsson, 2015; Terblanche et al., 2015).

Pinpointing possible mechanisms by which higher levels of colour pattern diversity may contribute to increased dispersal capacity, and differ between pest and non-pest species, goes beyond the scope of this study. However, animal colour patterns are genetically, developmentally and functionally associated with several other phenotypic characteristics and aspects of individual performance (McKinnon & Pierotti, 2010; McLean & Stuart-Fox, 2014; True, 2003). It has therefore been hypothesized and empirically confirmed that species with polymorphic or variable colour patterns have broader niches, are able to utilize a broader range of available resources and can cope with a greater diversity of environmental conditions (Forsman, 2016; Forsman, Ahnesjö, Caesar, & Karlsson, 2008). Variable colour patterns can also offer protection for individuals and populations from predation (Bond & Kamil, 2002; Karpestam, Merilaita, & Forsman, 2014, 2016). In the case of the association of variable colour pattern with long-distance dispersers and with agricultural pests indicated by our present results, it can be surmised, based on the same line of argument as outlined in Forsman et al. (2008), that more variable species are more likely to encompass at least some genotypes and phenotypes capable of withstanding the challenges and risks associated with dispersal across heterogeneous landscapes and novel selective regimes. This interpretation is further supported by the findings that species of moths with more variable colour patterns show faster northward range expansions in Sweden during the past 40 years (Forsman et al., 2016), have a lower extinction risk (Betzholtz et al., 2017), and also have larger continental range size distributions (Franzén et al., 2019).

Based on our existing data, we cannot ascertain whether variable colour pattern is a cause or an effect of high dispersal capacity. Theory and empirical evidence concur that dispersal and gene flow generally contribute to increased genetic and phenotypic diversity within populations (Charlesworth & Charlesworth, 2017; Slatkin, 1993; Tinnert, Hellgren, Lindberg, Koch-Schmidt, & Forsman, 2016; Yildirim, Tinnert, & Forsman, 2018). Accordingly, non-resident species recorded on the island may have variable colour patterns because they have a high capacity for long-distance dispersal and have been influenced by divergent selection in diverse environments. In the same vein, it is possible that the association of variable colouration with dispersal indicated by our present results reflect in part an underlying association of variable colouration with population density (Betzholtz & Franzén, 2013; Forsman et al., 2015), with species that are abundant on the mainland possibly contributing more dispersers. It should be emphasized here that, despite being of scientific interest, identifying the underlying mechanisms and direction of causation is not essential to evaluate the utility of variable colouration as a proxy for dispersal capacity and help identify potential agricultural insect pests.

Besides pointing to a positive effect of variable colour patterns, our analysis indicated that dispersal capacity increased with

duration of the flight period. This is not surprising because a longer lifespan also means that individuals may disperse longer distances. This can happen if dispersal is the sum of many short individual movement bouts, or by subsequent generations in multivoltine species. Additionally, it can be hypothesized that both the likelihood of deteriorating conditions that induce emigration and the likelihood of favourable weather conditions that allow for long-distance dispersal (i.e., windows of opportunity) accumulate over time. However, reliable information on length of the flight period may not be as easily accessible for many taxa, compared with data on colour pattern variation.

We also found that most noctuid pests (76%, 16 out of 21 species) had high capacity for long-distance dispersal. Terblanche et al. (2015) highlight that one of the most interesting areas of ongoing research in agricultural pests involves estimating maximum dispersal distances as it impacts the damage caused by the insect pest, as well as their distribution, and they suggest the use of multiple estimation methods is recommended to gain a higher understanding of dispersal potential in insect pests. Our data are interesting from this perspective because we show estimations of dispersal distances from the wild, and indicate that distances covered are generally longer than presented for agricultural pests in many earlier studies (Mazzi & Dorn, 2012). These findings may add to a better understanding of factors that influence long-distance dispersal in pest species, and may also aid to improve forecasts of pest range expansion dynamics and outbreaks (cf. Battisti & Larsson, 2015).

To conclude, our results identify inter-individual variation in colour pattern as a possible, easy-to-sample and cost-effective way of estimating dispersal capacity. Importantly, we estimated dispersal capacity in the wild on a spatial scale that is relevant for modelling population dynamics and range shifts of species in fragmented and changing landscapes. Our findings are thus of applied value in that they may be used when devising conservation measures of species and habitats. Further, our findings also present rare evidence of long-distance dispersal of agricultural pests in the wild, and further corroborate that many, but not all, pest species have high dispersal capacity (cf. Terblanche et al., 2015). This may be a useful finding when integrated pest management strategies under different scenarios of range expansions and climate change impact are developed (Lindström & Lehmann, 2015). Whatever the underlying processes responsible for the associations reported here, it seems that colour pattern variation encapsulates a wide range of mechanisms and features related to long-distance dispersal and the capacity for rapid population growth in moths. We encourage studies in other taxa to further evaluate the generality of our findings.

CONFLICT OF INTEREST

The authors declare that no conflicts of interest of any kind exist.

AUTHORS' CONTRIBUTIONS

PEB and MF conceived the research. PEB collected the data, and MF and AF performed the statistical analyses. All three authors contributed to the writing and approved the final version.

DATA ACCESSIBILITY

Data is provided in Supporting Information I-III.

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