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Applying the stress-gradient hypothesis to curb the spread of invasive bamboo

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Abstract

1. The stress-gradient hypothesis (SGH) provides a conceptual framework for explaining how environmental context determines the nature of biotic interactions. It may be also useful for predicting geographic variability in the effect of management interventions on biological invasions. We aimed to test hypotheses consistent with the SGH to explain context dependency in bamboo invasion of secondary forests in Japan, and establish a predictive understanding of forest management impacts on invasion.

2. We use *a priori* physiological knowledge of invasive giant bamboo, *Phyllostachys bambusoides*, to generate hypotheses consistent with the SGH. We modelled variation in giant bamboo occupancy within 810 secondary forest plots across the broad environmental gradients of Japan using a national vegetation database.

3. Consistent with the SGH, we find that the effect of tree canopy cover on bamboo occupancy depends on interactions between solar radiation and mean annual temperature. In cool regions with high solar radiation – stressful conditions for bamboo – shade cast by dense canopies facilitates invasion. However, in warmer regions that are more benign, dense canopies tend to inhibit spread via competition for light, space and other resources.

4. We used our findings to characterise geographic variability in the effect of forest thinning, a widespread management intervention used to enhance forest biodiversity, on the risk of bamboo spread into secondary forests in Japan. Thinning forest canopies to increase understorey light radiation should limit bamboo spread in cooler regions, while tree planting to increase canopy shade should limit bamboo spread in warmer regions. We provide evidence that the SGH can inform practical recommendations for invasive species control.

Key words: bamboo, competition-facilitation, Japan, light stress, photo-inhibition, vegetation management, invasive alien plant species.

要旨

1. ストレス勾配仮説（SGH）は、環境条件が生物学的相互作用の性質をどのように決定するかを説明するための概念的枠組みを提供するものであるが、この仮説は生物学的侵入に対処するための管理の効果の地理的変異を予測する際にも役立つ。本研究では、日本の二次林におけるタケ類の侵入に関する状況依存性（地域依存性）を説明するために、SGH に合致する仮説を検証し、森林管理が生物学的侵入に与える影響を予測可能なものとする知見を得ることを目的とした。

2. 我々は、日本に侵入してきたマダケ類の一種であるマダケ（*Phyllostachys bambusoides*）の生理的情報を用いて、SGH に整合的な仮説を立てた。本研究では、全国植生データベースを用いて、日本の広範な環境勾配にまたがる 810 の二次林区画内でのタケ類（マダケ属）の占有率の地理的変異をモデル化した。

3. SGH で予想される通り、樹冠率がタケ類の占有率に及ぼす影響は、日射量と年間平均気温に依存することがわかった。日射量の多い冷涼な地域（タケ類にとってストレスが大きい環境）では、樹冠が密集していることで日陰ができ、タケ類の侵入が促進されることが予測された。一方で、よりタケ類の生息に適した日射量の多い温暖な地域では、樹冠が密に覆われた場所では光や空間、資源をめぐる種間競争が激化し、タケ類の侵入が抑制されることが示された。

4. 上記の結果を基に、森林の生物多様性を向上させるために広く行われている間伐が、二次林におけるタケ類の分布拡大リスクに及ぼす影響にどれくらい地理的変異があるのかを調べた。その結果、冷涼な地域では、樹幹を減らして下層の光量を増加させることでタケ類の分布拡大を抑えることができ、暖かい地域では、日陰を増やすために植樹を行うことでタケ類の分布拡大を抑制できることが予測された。本研究結果は、SGH が侵略生物の制御のために実践的な提言ができることを示している。

キーワード：タケ、競争促進、日本、光ストレス、光阻害、植生管理、侵略的外来植物種

Introduction

Worldwide, invasive species threaten the capacity of ecosystems to sustain biodiversity and deliver critical ecosystem services (Pyšek et al., 2012). To effectively prevent and control their negative impacts now and in the future, a predictive understanding of invasion success is required (González-Moreno, et al., 2014). However, predicting invasion success is challenging due to its contingency on myriad interdependent abiotic and biotic drivers (Pyšek et al., 2020). While abiotic conditions such as climate can explain the distribution of invasive species at macro-ecological scales (Ficetola et al., 2007), patterns of invasion often appear geographically idiosyncratic even within hospitable climatic ranges (Holmes et al., 2010). Such patterns are suggestive of interactive effects of broad-scale environmental conditions with local biotic interactions (González-Moreno et al., 2014). Both negative (e.g. competition) and positive (facilitation) biotic interactions are well-recognised in invasion ecology (Cavieres et al., 2005; Lucero et al., 2019), and the nature of these interactions have been shown to vary across broad extents (Early & Keith, 2019). However, the drivers of this variability, or 'context dependence', have yet to be characterised for a range of taxa and ecosystems (Chamberlain et al., 2014).

The stress-gradient hypothesis (SGH) provides a unifying conceptual framework that can help explain how environmental context determines whether native species inhibit or facilitate invasion (Bruno et al. 2003). The SGH predicts that the relative frequency or strength of facilitation and competition will vary inversely across abiotic stress gradients (Bertness & Callaway, 1994; Callaway & Walker, 1997). Under increasingly stressful conditions, the presence, size and density of neighbouring 'nurse' species can become increasingly important in facilitating the persistence of a species in conditions that would otherwise not be tolerated, enabling the latter species to expand its realised niche (Bruno et al., 2003). For instance, cushion plants can facilitate recruitment of other herbaceous species in alpine environments by buffering temperature extremes (Cavieres et al., 2005). Conversely, under benign physical conditions, interspecific competition with neighbours may increase, such that otherwise facilitating 'nurse' species become competitors instead (Bertness & Callaway, 1994; Callaway & Walker, 1997; Brooker et al., 2008). While the SGH has successfully explained variability in biotic interactions in stressful settings, such as alpine, intertidal, and early successional environments (He et al., 2013), there have been few applications, however, to applied questions relevant to ecosystem management, except for the deliberate use of nurse plants as restoration tools in harsh environments (Guignabert et al., 2020). However, management efforts that alter the abundance or distribution of nurse species could also have unintended consequences for invasive species, which the SGH could help to mitigate.

Here, we apply the SGH to predict plant invasion success in response to forest management across the broad environmental gradients of Japan. Specifically, we use the SGH and *a priori* physiological knowledge of invasive giant bamboo *Phyllostachys bambusoides,* to generate hypotheses about bamboo occupancy, and apply this to fine-scale forest survey data collected across the broad environmental gradients of Japan. Importantly, we show how the SGH could help elucidate where species interactions should be considered when formulating local forest management practices that involve changes to the abundance of species facilitating or competing with invaders.

Bamboo invasion is an ideal case study for testing the applicability of the SGH in an applied context. First, the distributional limits of *Phyllostachys* species in both their native and non-native ranges are strongly temperature-dependent (Song et al., 2017; Takano et al., 2017). Within these limits, its occupancy within secondary forests is highly variable (Isagi and Torii 1997; examples in Appendix S1), which could reflect interactions between biotic and abiotic drivers. Second, physiological studies of multiple *Phyllostachys* species under controlled settings have demonstrated that photoinhibition (light-induced decline of photosynthesis) occurs under moderate light intensities at low temperatures, but can be ameliorated at warmer temperatures or under shade (Van Goethem et al. , 2013; Van Goethem et al., 2015; Lou et al., 2018). In other words, physiological understanding of *Phyllostachys* points to interactions among multiple abiotic drivers (Maestre, Callaway, Valladares, & Lortie, 2009; He & Bertness, 2014), suggesting observed fine-scale geographic variation in its invasion success might be consistent with the SGH. Specifically, we hypothesised that in cool and high-light environments, the shade cast by forest canopies could exert positive (facilitative) effects on bamboo invasion under stress (Hypothesis 1, Fig.1 C). However, under benign conditions corresponding to warmer temperatures, we hypothesised that dense canopies might exert negative effects due to competition for space, nutrients or available light (Hypothesis 2, Fig.1D). We made the explanatory prediction (*sensu* Mouquet et al., 2015) that when under high light, effects of photoinhibition would manifest as a shift in the thermal niche of bamboo along a gradient of canopy cover, consistent with the SGH.

Materials and methods

Study system and taxa

Giant bamboo (*Phyllostachys*) species were introduced to Japan from China around three centuries ago for their culm woods and edible shoots (Isagi & Torii, 1997). Bamboo forests were widely planted across western and central Japan as part of production landscapes known as ‘satoyama’, mosaics of secondary broadleaved forests managed as coppices, residential areas, paddy fields and grasslands (Takeuchi, 2010). Rapid economic growth, the introduction of new fuels and large-scale urban development during the 1950s-60s resulted in widespread satoyama abandonment. Without active management, bamboo plants extend their rhizomes laterally, driving bamboo forest expansion into adjacent secondary forests that were historically managed as coppices, but are now abandoned (Fukamachi et al., 2001). Carbohydrates from the clonal adult root system can sustain the growth of new bamboo shoots, that are initiated every summer and emerge aboveground the following spring, making them shade-tolerant and able to invade forests with dense canopies 2016). Bamboo invasion can inhibit regeneration, decimate understorey plant communities and alter soil chemistry (Nakai & Kisanuki, 2006).

Ecophysiology of *Phyllostachys* spp.

Photosynthetic and growth rates of bamboo are strongly temperature-dependent. *P. bambusoides* can achieve 90% of its maximum photosynthetic rate when its leaves are warm (13.8-24.2 °C), but only 50% when its leaves are cooler (6.2-32.1 °C) et al., 2008). Temperature moderates the impact of light stress in *Phyllostachys* species (Van Goethem et al., 2013). *Phyllostachys* species exhibit photoinhibition, light-induced decline of photosynthetic activity due to excess excitation energy, even under relatively low light intensities (Van Goethem et al., 2015; Lou et al., 2018). Factorial experiments have demonstrated strong photoinhibition of *Phyllostachys* species under unshaded cold conditions (3-10°C), but weak photoinhibition in both unshaded warm (13-20°C) conditions and shaded cold conditions (Van Goethem et al., 2015). In contrast to warm conditions, thermal dissipation of excess excitation energy is not possible under cold conditions. *Phyllostachys* species photosynthesise year-round (Wang et al. 2016), with photosynthetic capacity increasing from a spring minimum, due to the combination of low air temperatures and increasing light irradiation, to an autumn maximum (Gratani et al 2008; van Goethem et al. 2014). These results suggest that the degree of shade cast by dense forests might have important facilitative effects at low temperatures, protecting *Phyllostachys* from photoinhibition. We therefore set out to test the hypothesis that the effect of canopy cover on bamboo invasion probability would depend on, i.e. interact with, light intensity and temperature (Figs 1C &1D). In regions with warmer temperatures, where growth is less limited by photoinhibition, canopies could plausibly exert negative effects due to competition for space, nutrients or light.

Vegetation data

We retrieved bamboo incidence data from the vegetation survey database of Japan, provided by the Biodiversity Center of Japan (http://gis.biodic.go.jp/webgis/files/). This dataset consists of vegetation and geospatial data for >55,000 plots surveyed between 2000-2015, compiled from a range of sources, comprising species presence/absences, in addition to the percentage cover and height of vegetation. For plots located in forest habitats, consultants recorded the percentage cover of canopy, and soil properties. We focussed on *P. bambusoides*, which was the most prevalent in secondary deciduous forests, and refer to it as 'bamboo' from hereon.

Environmental data

We selected potential explanatory variables of bamboo occupancy based on existing empirical studies (Suzuki and Nakagoshi 2008, Someya et al. 2010, Suzuki 2015; Table S2). Climatic variables were available at a 1-km resolution (Japan Meteorological Agency, 2010), and included temperature, rainfall, solar radiation, sunshine duration and snow depth based on annual averages between 1971-2000. For temperature, we calculated average annual values of monthly minima, means and maxima, in addition to obtaining values for the coldest and warmest months. We calculated two distance metrics to characterise the likelihood of propagule dispersal by vegetative spread. Distance to forest edge was expected to drive down invasion probability, as bamboo invades by spreading from bamboo forest into adjacent habitats, resulting in bamboo forest expansion. Distance to road serves as a proxy of secondary forest abandonment, because secondary forests and bamboo forests are less likely to be managed if far from roads and relatively inaccessible (Y. Kobayashi & Nakamura, 2018). Indeed, distance to road has been shown to be positively correlated with expansion rates (Suzuki & Nakagoshi, 2008; Suzuki, 2015).

Local topographical variables have been shown to affect bamboo spread, including slope and measures of aspect (Suzuki and Nakagoshi 2008), and were calculated using a 30-m digital elevation model (Table S2). Invasion of secondary forest by bamboo is more likely to occur in abandoned areas where bamboo and secondary forest management have ceased (Suzuki, 2015). In the absence of fine-resolution forest management data and assuming that bamboo and secondary forest abandonment coincide with agricultural abandonment, we used the extent of abandoned agricultural land (paddy fields, farmland, pasture) available at a 5-km resolution (Osawa et al., 2013), following Suzuki (2015). It has been suggested that stand structure might be important in determining the likelihood of giant bamboo spread (Isagi & Torii, 1997), so measures of forest canopy cover and forest type (i.e. whether dominated by an evergreen or deciduous tree species) were extracted from the plot database. We also considered survey year as a potential explanatory variable, as a correlate of time since widespread landscape abandonment. Minimum residence time (Wilson et al., 2007) is not relevant in this case study because all bamboo plantations were deliberately established and commercially productive before abandonment such that their residence time was effectively uniform across the country. The more relevant time period, therefore, is year of abandonment, which we have represented with distance to road as a proxy.

We translated our hypotheses concerning regional and local variables, and their interactions, into statistical models (Spake et al., 2019a). Consistent with the SGH (Figure 1), we hypothesised a three-way interaction between solar radiation, temperature and canopy cover. Aspect and slope can moderate the amount of solar radiation and hence the microclimate of a locality (Ashcroft & Gollan, 2013). Suzuki & Nakagoshi (2008) found differences in the importance of slope in limiting bamboo expansion across two regions varying in precipitation and temperature variables (Suzuki & Nakagoshi, 2008), while Torii *et al.*, (2005) suggested that sunshine or solar radiation interacts with slope (Torii et al., 2005). We therefore hypothesised interactions between these topographical and climatic variables.

Vegetation plot stratification

We required a subset of plots, surveyed in secondary forests, which were plausibly at risk of invasion by bamboo over the sampling period. This was to ensure that our absence records used in our models were 'real' absences and not simply due to plots being outside of the dispersal range of the species. First, we selected plots with complete data available for climate variables, canopy dominant species and canopy cover (n = 16,556), and excluded plots from the southern subtropical islands due a low sample size of plots occurring at outlying temperature values, and differences in management in these regions (n = 16,156; Figure S3.2).

Second, we selected plots that were plausibly at risk. The susceptibility of an ecosystem to invasion depends on propagule pressure, abiotic conditions and biotic interactions (Catford, Jansson, & Nilsson, 2009). For transparency, a detailed account of our plot stratification procedure is in Appendix S3.Not all of the >16,156 plots were at risk of invasion by bamboo during the survey period (2000-2015). We considered plots at risk if they were close to planted bamboo forest, according to distance and elevation. For example, bamboo forests (vegetative propagule sources) were planted predominantly across central and western Japan, therefore plots in northern Japan were not at risk during the survey period. To identify such plots, we used a digital elevation map and a land cover map that distinguished bamboo forests (The 5th Basic Survey of Natural Environment Conservation by the Ministry of Environment of Japan; http://www.biodic.go.jp/trialSystem/shpddl.html). We considered plots within a distance of 1-km of mapped bamboo forests to be ‘at risk’ of invasion; 99% of vegetation plots containing bamboo were within 1000-m of mapped bamboo forests (Figure S3.3). Plot elevation ranged between 0 and 2735-m. We selected all plots below an elevation of 750-m, to identify plots near to residential areas, i.e. at elevations below which bamboo forests were extensively planted; 99% of plots containing bamboo were below 750-m). This yielded 10,287 plots (Figure S3.3).

The environmental characteristics of a site must be hospitable for invasion to occur (Catford et al., 2009), so we further selected plots with abiotic characteristics within the ranges that were hospitable to bamboo. We selected only deciduous plots by matching the canopy dominant with the phenology type (deciduous/evergreen) of the TRY database (Kattge & et al., 2019). Only deciduous plots were selected to limit covariation between temperature and phenology type in Japan (Kira, 1991; Suzuki et al., 2015), which in turn could be confounded with an effect of canopy cover on invasibility (n = 5,906, Figure S2.4). Next we selected plots dominated by tree species within which bamboo was present in at least 1% of plots dominated by that species, in order to select forest types, with corresponding microclimates and management regimes, at risk. Finally, we stratified plots based on the range of abiotic variables observed within plots where bamboo was present. We did this by selecting plots that occurred within the range of plots that contained bamboo for mean annual temperature, rainfall and solar radiation (Figure S3.6).

In total, this multi-step plot selection procedure yielded 810 plots dominated by deciduous broadleaved tree species, of which 67 contained bamboo, distributed across Japan. Hereon we refer to these as secondary forests *sensu lato*, due to the history of deciduous broadleaved forest exploitation in Japan (Totman, 1989).

Statistical analysis

All analyses were carried out using R version 3.5.3 (R Core Team, 2019). Data exploration was carried out following the protocol described in Zuur et al. (2010) (see Appendix S4). Covariation among survey year and temperature suggested that vegetation survey campaigns were conducted progressively across space in successive sampling years. To avoid collinearity, we excluded survey year from the global models (we retained temperature, reflecting our hypotheses, Figure 1). Snow depth was also excluded due to moderate collinearity with temperate and solar radiation. Moreover, the more relevant temporal variable for bamboo invasion is year of abandonment, which we have represented with distance to road as a proxy (which did not covary with temperature). Distance measures (to forest edge and nearest road), and agricultural abandonment required log transformation to reduce the effect of outliers.

To quantify how the probability of secondary forest invasion by bamboo varies with regional, landscape, and local-level drivers (Table S2) and their interactions (Figure 1), we fitted generalised linear models against a binomial distribution with a clog-log link function to the bamboo occupancy (presence/absence) data, due to unbalanced presences and absences (Zuur et al., 2009). Our modelling approach had two stages: exploration and multi-model inference (detailed in Appendix S5).

Stage 1: Exploring the shapes of predictor relationships

While we had formulated *a priori* hypotheses about the effects of environmental drivers (Figure 1), we did not know the exact shape of relationships, i.e. whether to include a quadratic term for temperature, or whether annual temperature means, minima or maxima would provide superior fit, necessitating model comparison (Fisher et al., 2018).

We created global models that contained the additive main effects of slope, northness and eastness, temperature variables, distance to road, distance to forest edge, in addition to a three-way interaction between temperature, solar radiation and canopy cover, and an interaction between solar radiation and slope as hypothesised (see Appendix S6 for details of the global model). A log transformation of plot size was included as an offset to adjust for variation in plot size.

Global models differed in the substitutions of temperature variables, whether annual means minima or maxima were included. They were not included in the same model due to high collinearity (e.g. mean and maximum annual temperature had $\rho>0.8$, Appendix S5). We also ran models with and without an additional quadratic term for temperature. From these global models, we generated full, ‘all subsets’ sets of nested models, with the dredge function from package MuMIn (Bartoń, 2018; see Appendix S5), to be compared with Akaike's Information Criterion (AIC). All variables were centred and scaled to unit S.D. prior to model fitting (Grueber et al. 2011).

This initial model exploration demonstrated that the hypothesised interactions, and a main effect of a quadratic term for mean annual temperature, were supported by the data, i.e. were included in models with $\Delta\text{AIC}<2$. Prior to multi-model inference, we therefore restricted the model set to models containing the hypothesised interactions, and both a linear and quadratic term for mean annual temperature. This was done because the sign and magnitude of regression coefficients can change considerably across models depending on the presence or absence of interactions and polynomial terms, precluding multi-model inference (Cade, 2015).

Stage 2: Multi-model inference

We identified a 'top model set' containing models with ΔAIC<6 (Richards, 2005; Harrison et al., 2018). The goodness of fit of these models (pseudo-R^2) was calculated following Nagelkerke (1991). We applied natural model averaging of parameter estimates for each predictor (Nakagawa & Freckleton, 2010; Grueber et al., 2011). Natural averaging was done instead of zero averaging, where parameter estimates (and errors) of zero are substituted into models where the given parameter is absent, because our aim was not to rank the importance of predictor variables (Nakagawa & Freckleton, 2010), but to model biologically meaningful responses.

We graphed the relationships between covariates and predicted values of occupancy using the predict.glm() function, using the average predicted values from the models in the top model set, following Cade (2015). We expected the thermal niche of bamboo to shift with increasing canopy cover under high solar radiation, consistent with the SGH (see above). To visualise a potential shift in the realised thermal niches of bamboo, we plotted the predicted probabilities of bamboo occupancy (averaged across the top models) along a temperature gradient in the presence of relatively strong and weak biotic interactions, corresponding to secondary forests with dense (100%) and more open (60%) canopy covers, respectively. We plotted thermal niches for bamboo at relatively low and high levels of solar radiation (120 and 135 $\mathrm{MJm^{-2}}$), with R package ggplot2 (Wickham, 2016).Model assumptions were verified by plotting residuals versus fitted values, versus each covariate in the model and versus covariates not in the model (e.g. survey year) (Zuur et al., 2009) using the DHARMa package (Hartig, 2018) for each model in the top model set. We also assessed the residuals for temporal and spatial dependency. Model validation indicated all assumptions were met (Appendix S7). Generalised variance inflation factors were calculated to check for collinearity. Because predictors were centred and scaled, we interpreted the relative magnitudes of averaged regression coefficients as a measure of relative, standardised effect sizes (Schielzeth, 2010).

Application to forest management in Japan

To identify where biotic interactions (i.e. shade from forest canopy) should be considered when implementing forest management, we mapped the spatial heterogeneity of the effect of thinning (i.e. reductions in canopy cover) on bamboo invasion across Japan. To do this, we first mapped the predicted occupancies of bamboo in space using 1-km×1-km pixel-level values of the climate variables that were important in predicting occupancy. Occupancies were predicted for 100% and 60% canopy cover, corresponding to a typical reduction in stand volume that is incurred during secondary forest thinning in Japan (Spake et al., 2019b). Occupancies were only predicted within the sampled range of predictor variables, for pixels within 1-km of existing bamboo forest, where secondary forests are plausibly at risk. Predictions were made for each model in the top model set while holding all other covariates at their median values, and averaged across models for each pixel. Following Spake et al. (2019a), we then estimated and mapped an effect size, the risk difference (the difference in average occupancy probabilities) between forests with 100% and 60% canopy cover, to represent the direction and magnitude of the effect of thinning. Positive values correspond to increases in the probability of bamboo occupancy following a reduction in canopy cover, while negative values corresponded to a decrease in occupancy probability.

Results

We found that both regional climate, landscape and local variables and their interactions explained variation the probability of bamboo occupancy in secondary deciduous forests across Japan (details of multi-model inference and parameter estimation in Appendix S6).

Models within the top model set (ΔAIC<6) explained 21-24% of variation in bamboo occupancy (Table S6.1). The averaged model predicted occupancy to decline weakly with rainfall and distance to road (Figure 2). Occupancy declined with hill slope, with a more strongly negative relationship observed in regions with higher solar radiation (Figure 2). Occupancy was best explained by annual means of monthly average temperatures ('average temperature' from hereon), with a main effect of a quadratic term

A three-way interaction between average temperature, solar radiation and canopy cover explained variation in bamboo occupancy (Appendix S6; Figure 3). Consistent with the SGH and our hypotheses specific to bamboo invasion (Figure 1), we observed a shift in the thermal niche of bamboo with canopy cover under high light intensity. At relatively low levels of solar radiation, canopy cover had little effect on the thermal niche of bamboo in secondary forests, shown by the similarity of bamboo probability distributions with different levels of canopy cover (Figure 3a). In regions with high light intensity however, canopy cover became an important facilitator of bamboo occupancy, with bamboo more able to establish in secondary forests at lower temperatures under dense canopies, than in forests with more open canopies (Fig 3b). However, at higher temperatures, dense canopies become more limiting than open canopies, with bamboo occupancy tending towards being more likely in open (60% cover) than closed (100%) canopies beyond 15°C (Figure 3b).

The interactive effects of canopy cover with solar radiation and temperature translated to high spatial heterogeneity in the effect of canopy cover – and hence the effectiveness of thinning – on bamboo occupancy across Japan (Figure 4a-c).

Discussion

Our study of *P. bambusoides* invasion in Japan demonstrates that the stress gradient hypothesis (SGH) provides a valuable framework for applied invasion ecology: it can help explain the context dependence of invasion across locations, and can be used to guide management. Implicit to the SGH is the integration of ecophysiology, species interactions and biogeography, which – although inherent to the niche concept (Helmuth et al., 2005) – are rarely integrated (Wiens, 2011; Godsoe et al. 2017). Here we have documented a thermal niche shift of bamboo occupancy under high solar radiation (Figure 3b): when under dense canopies, the optimal niche of bamboo shifts to several degrees lower. At low temperatures, bamboo cannot establish in secondary forests with sparse canopies where it is prone to light stress. At higher temperatures, where light stress is ameliorated, dense canopies can be limiting to its spread (consistent with hypotheses in Figure 1). This apparent contradiction explains why bamboo invasion success is highly variable among deciduous secondary forests in Japan (Isagi & Torii, 1997). Our study suggests that the SGH holds much potential for applied fields of ecology that aim to inform conservation and management plans.

The SGH has been subject to debate since its conception, motivating numerous refinements since its conception (e.g. Maestre et al., 2009). Observed exceptions from the SGH have been attributed, among other factors, to multiple, uncorrelated stress gradients that can ‘cancel out’ SGH effects (Maestre et al., 2009). Controlled, factorial experiments have therefore been widely advocated to identify actual exceptions to the SGH rather than those due to failures to meet its underlying assumptions (Maestre et al., 2009; He & Bertness, 2014). So while the SGH makes predictions about species’ niches – and is therefore inherently a question of biogeographic scale (Wiens, 2011) – most studies have been conducted across limited extents (Ziffer-Berger et al., 2014), with communities compared across subjectively defined ‘high’ and ‘low’ stress conditions (He et al., 2013). Here we show that applying the SGH to field data spanning broad gradients helps explain context dependence in bamboo invasion, a ubiquitous phenomenon in invasion ecology (Catford et al. 2019, Pyšek et al. 2020). This yielded two main benefits. First, the SGH’s focus on the niche encourages integration of physiological knowledge into analyses, so that models are appropriately parameterised with necessary interactions. *A priori* physiological insight and hypotheses concerning the SGH led us to examine and reveal a three-way interaction among solar radiation, temperature and canopy cover. This allowed us to detect a thermal niche shift for bamboo under dense canopies (Figure 3). Such insights are difficult to obtain from typical correlative species distribution modelling, as these require little knowledge of the mechanistic links between an organism's physiology and their abiotic environment (Helmuth et al., 2005). Indeed, both physiological insight and biotic interactions are typically omitted from models that approximate species occupancy or abundance (Kearney & Porter, 2009; Staniczenko et al., 2017).

Our findings agree with experimental evidence and make sense mechanistically, with the degree of shade cast by dense forest canopies facilitating invasion at low temperatures, where thermal dissipation of excess excitation energy is not possible. Nevertheless, before implementing our findings into management, we suggest that manipulative mesocosm experiments in the field, designed to emulate this three-way interaction in forests, would be a useful intermediary to ground-truth that shading cast by forest canopies exerts facilitative and competitive effects under different abiotic conditions, and to confirm whether forest trees are competing with the bamboo for resources unmeasured in this study. This study could be carried out on existing bamboo forests, as annual expansion rates can be reliably estimated by rapid, one-time measurements of bamboo culms spreading from source bamboo forests (Kobayashi, Kitayama, & Onoda, 2018).

Second, the application of the SGH permits the characterisation of geographic variability in the magnitude, and even direction, of a widespread management intervention, forest thinning (Figure 4). While biotic interactions can challenge forecasts of community responses to climate change (Hillerislambers et al., 2013), these interactions also present management opportunities: the SGH can help characterise spatial variability in the effect of management.

Across Japan, forest thinning is widely used to enhance the biodiversity and recreational value of forests (Spake et al., 2019b). Incorporating the SGH into our analytical design revealed potentially adverse effects of forest thinning in cooler areas. Given that giant bamboo is projected to expand its range northwards in Japan with rising temperatures (Takano et al., 2017), thinning might reduce spread at these northern limits.

We expected distance to road to relate positively with invasion probability, due to its representation of the likelihood that a bamboo and/or secondary forest has been abandoned (Y. Kobayashi & Nakamura, 2018), and because distance to road has previously correlated positively with expansion rates in Japan (Isagi & Torii, 1997; Suzuki & Nakagoshi, 2008). On the contrary, we found a negative relationship with distance to road. This is likely due to differences in study design: here we investigated bamboo occupancy in secondary forest plots, while previous studies have measured annual expansion rates of existing bamboo forests into neighbouring vegetation (Appendix S1). Distance to road likely correlates with the occupancy of source bamboo forests, because bamboo forests were typically planted near roads and residential areas (Fukamachi et al., 2001). We did not detect an effect of our measure of agricultural abandonment, possibly due to this variable's coarse resolution (5-km) and consequent poor representation of bamboo and secondary forest abandonment, which varies at a finer scale than 5-km.

We found that hill slope increasingly related negatively to forest invasion with increasing solar radiation (Figure 2). Slope can modify the amount solar radiation received by a surface (Ashcroft & Gollan, 2013), but can also covary with soil types (Kamoshita, 1955). Suzuki & Nakagoshi (2008) compared drivers of bamboo forest expansion rates in two regions of Japan, and concluded that slope exerted a more strongly negative effect in the region with drier, less developed soils. We were unable to include soil variables in our analyses, as available soil type information was too inconsistent across plots to serve as a useful covariate.

Soil type and moisture are likely to directly drive bamboo occupancy and abundance (Takano et al., 2017), and also has the potential to mediate the effects of temperature extremes on plant communities (Fridley, et al. 2010). We recommend that future vegetation surveys in Japan adopt a systematic soil classification scheme, to permit the use of this covariate.

Tests of the SGH have been applied much less to diffuse, rather than species-specific interactions, despite their wider prevalence (Brooker et al., 2008), and rarely in forest ecosystems, which are not classically considered as extreme environments (He et al., 2013). However, our findings are consistent with tests of the SGH for species-specific interactions conducted across smaller extents. For example, Cavieres et al. (2005) found that seedling survival and net-photosynthetic rates of invasive *Taraxacum officinale,* were higher when growing within native cushion plants, *Azorella monantha*, than in open areas in the high-Andes (Cavieres et al., 2005). This suggests that the SGH may be broadly applicable across ecosystems and communities, and in invasion ecology. Given that rising temperatures are expected to increase the spread of invasive species, and have stronger positive effects on the performance of invasive than native plant species (Liu et al., 2017), future applications of the SGH present a promising way forward for predicting future species invasions – and how to mitigate them.

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Authors' contributions

RS and MS designed the initial analysis and collated the data. RS, MS, JC and FE further developed the conceptual ideas. RS analysed the data and wrote a first draft. All authors contributed substantially to revising the manuscript.

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Data Availability Statement

The data analysed have been archived at: https://figshare.com/s/991df7c65a1778c052a9 along with an annotated R script to reproduce the analysis. [Currently a private link, but will be made public if accepted for publication]. Vegetation plot data were from the Ministry of Environment's 'Natural Environment Information GIS' dataset (http://www.biodic.go.jp/chm/). Climate data are also publicly available (https://www.jma.go.jp/jma/indexe.html).

Figures

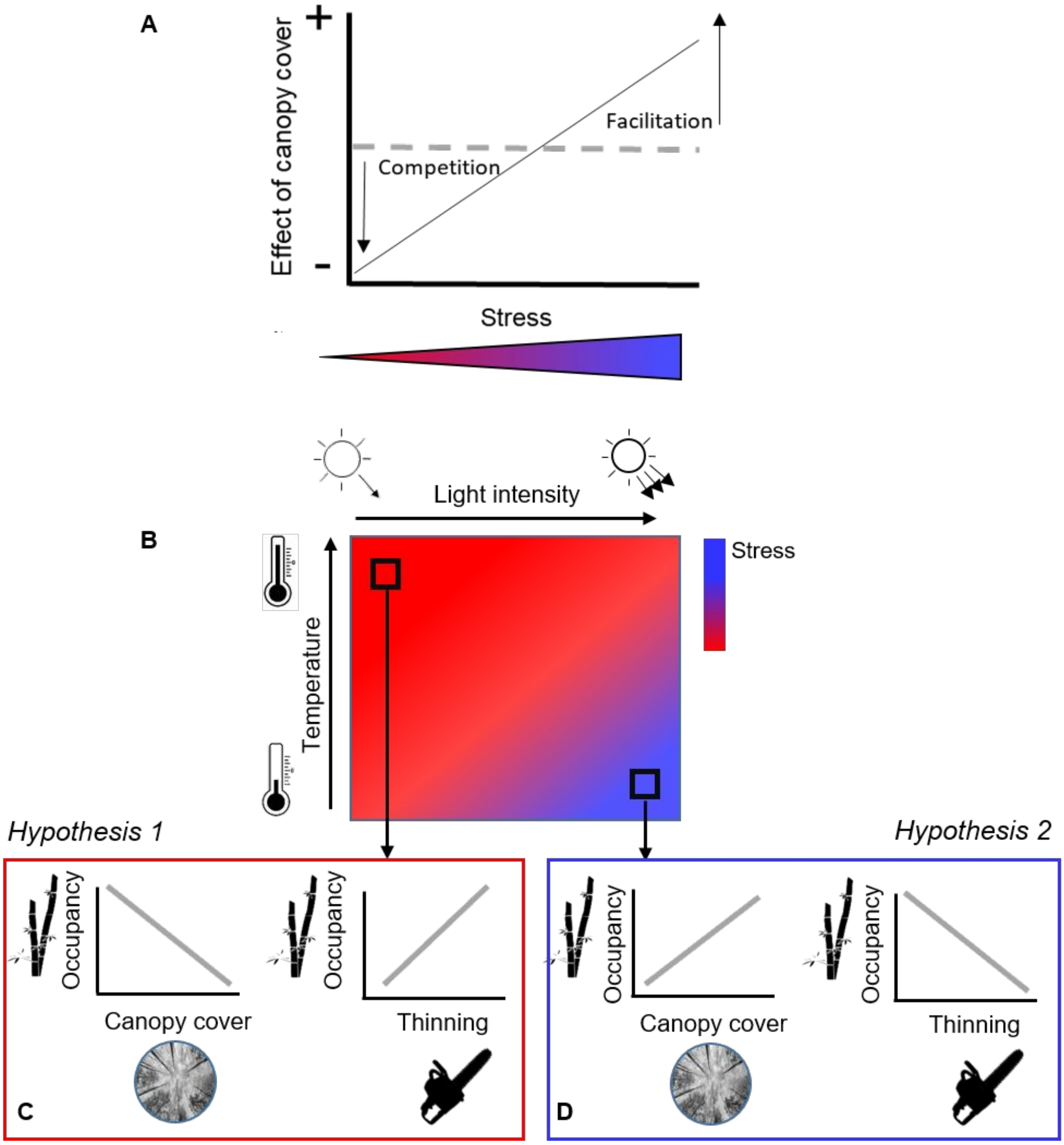


Figure 1. Conceptual figure representing hypotheses consistent with the stress-gradient hypothesis. A) The effect of canopy cover will change in direction across the stress gradient, determined by light intensity and temperature (B). C) Hypothesis 1: Under low stress (low light intensity + any temperature, or high light intensity + warm temperature), dense canopies may cause light to become a limiting resource, thus limiting bamboo establishment in secondary forests. Forest thinning should therefore increase the probability of invasion. D) Hypothesis 2: Under stressful conditions (high light that can cause photoinhibition + low temperature), the shade cast by dense canopies may facilitate establishment by protecting bamboo from light stress. Under these conditions, forest thinning should reduce the likelihood of invasion.

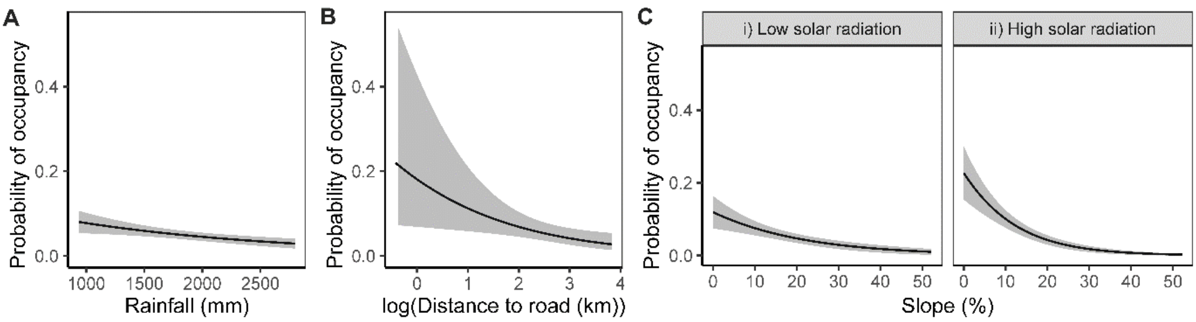


Figure 2. The probability of secondary forest invasion by bamboo (occupancy) consistently decreased with rainfall (A) and distance to road (B). Invasion declined with slope, this effect was stronger in regions with higher radiation (135 MJm^{-2}) than lower radiation (120 MJm^{-2}) (C). Relationships were graphed using predictions averaged across the top model set (ΔAIC<6), with other covariates variables held at their median. Shading shows average estimated standard errors.

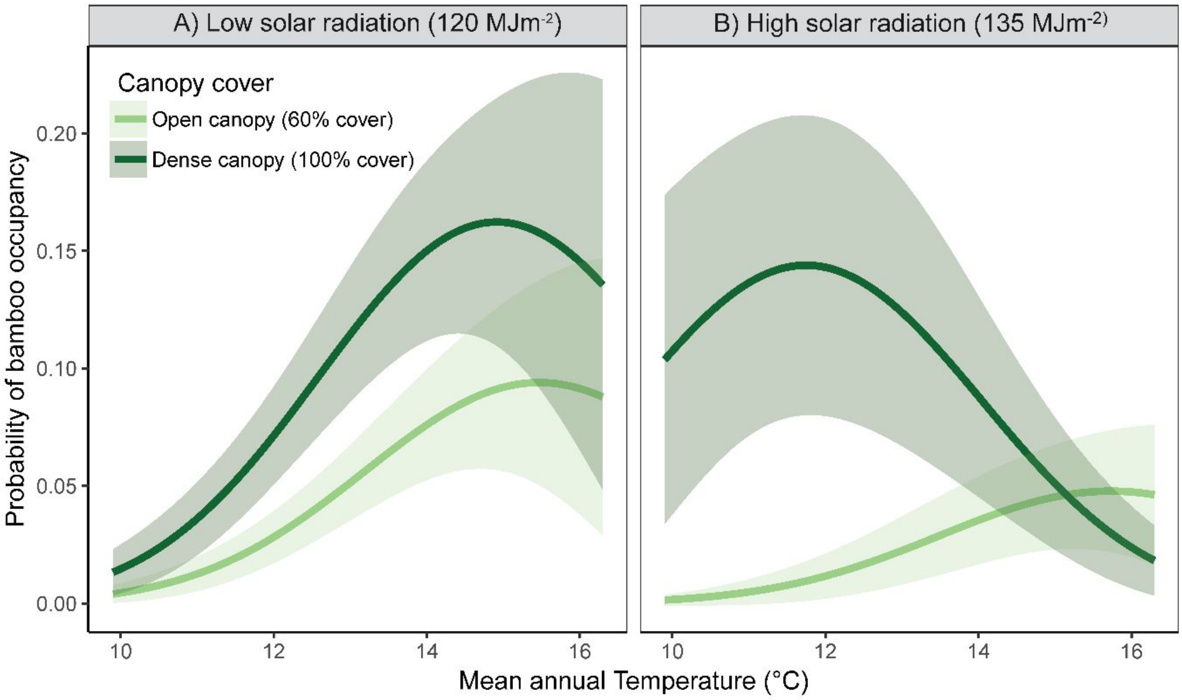


Figure 3. Realised thermal niches of giant bamboo under A) low solar radiation (120 MJm^{-2}) and B) high solar radiation (135 MJm^{-2}), under dense (100% cover, dark line) and more open (60%, light line) secondary forest canopies. Relationships were graphed using predictions averaged across the top model set (ΔAIC<6), with other covariates variables held at their median. Shading shows average estimated standard errors.

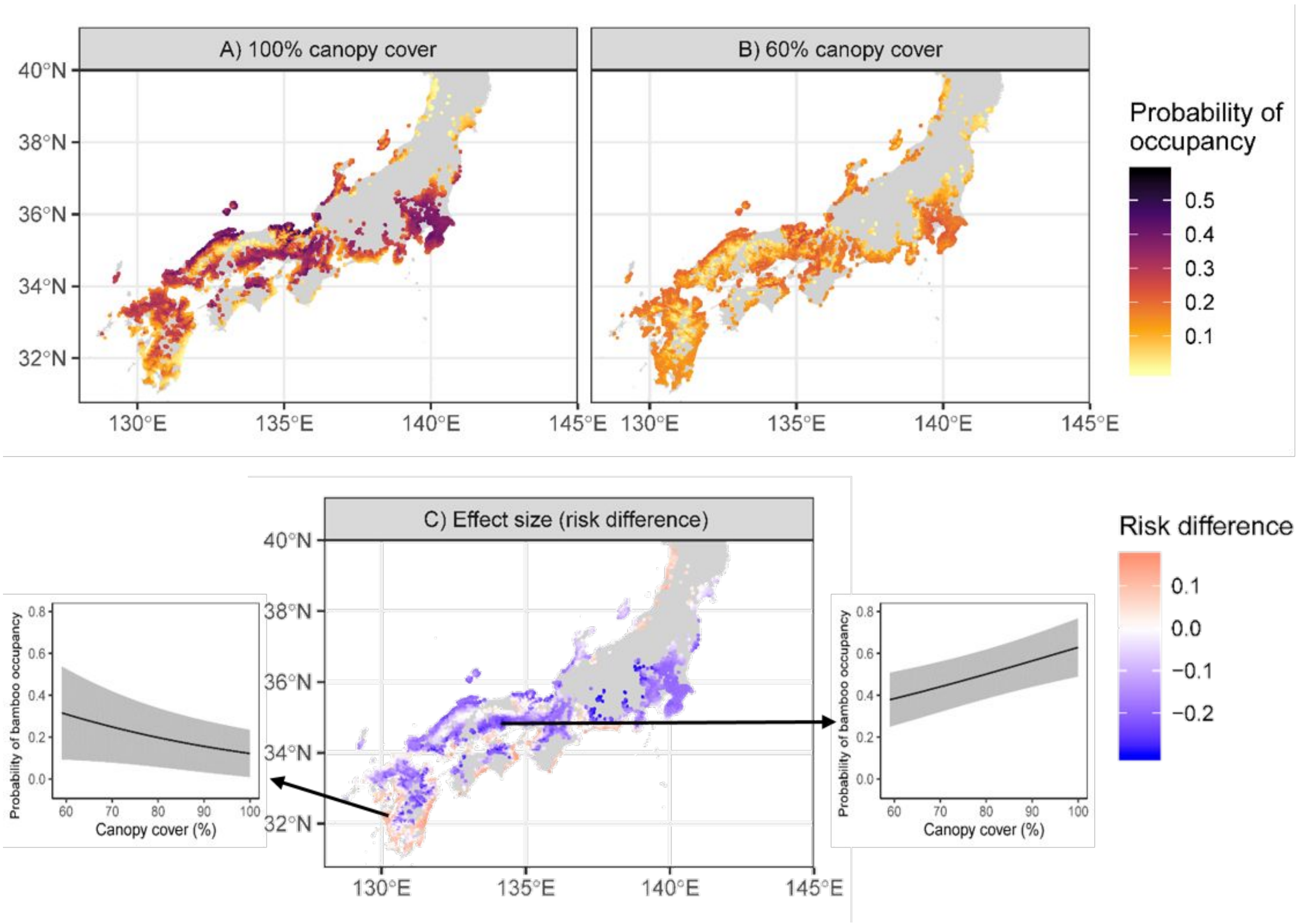
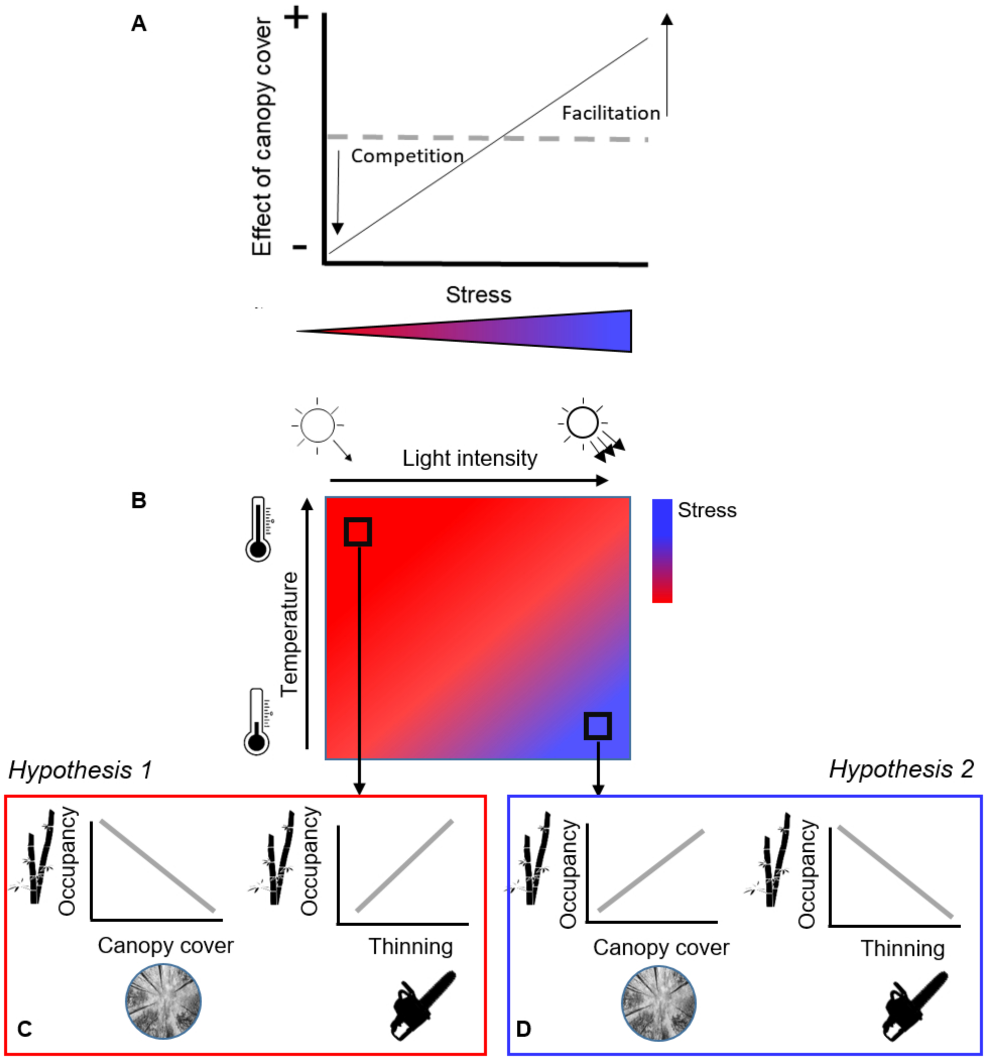


Figure 4. Spatial variation in *Phyllostachys bambusoides* occupancy, predicted by climate variables solar radiation, mean annual temperature and rainfall, for secondary forests under a) dense canopies (100% cover) and b) more open canopies (60%). C) Spatial variation in the effect of reducing canopy cover from 100% to 60% on predicted bamboo occupancy probabilities (the risk difference, i.e. occupancy difference between A) and B)). Positive values (red) correspond to increases in the probability of bamboo occupancy following a reduction in canopy cover, while negative values (blue) corresponded to a decrease in occupancy probability. Colour shading represents the strength of the effect. Inset are marginal changes in occupancy with canopy cover from two locations differing in solar radiation, rainfall, and temperature. Shown occupancy probabilities are averaged predictions from each model across the top model set (ΔAIC<6), using values of regional climate variables and other covariates held at their median.



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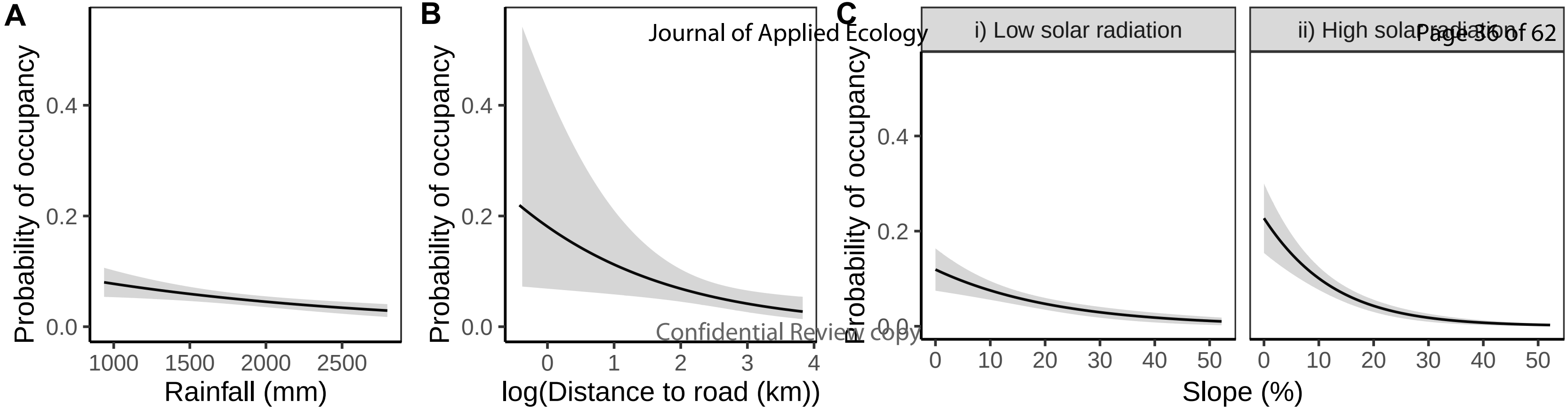
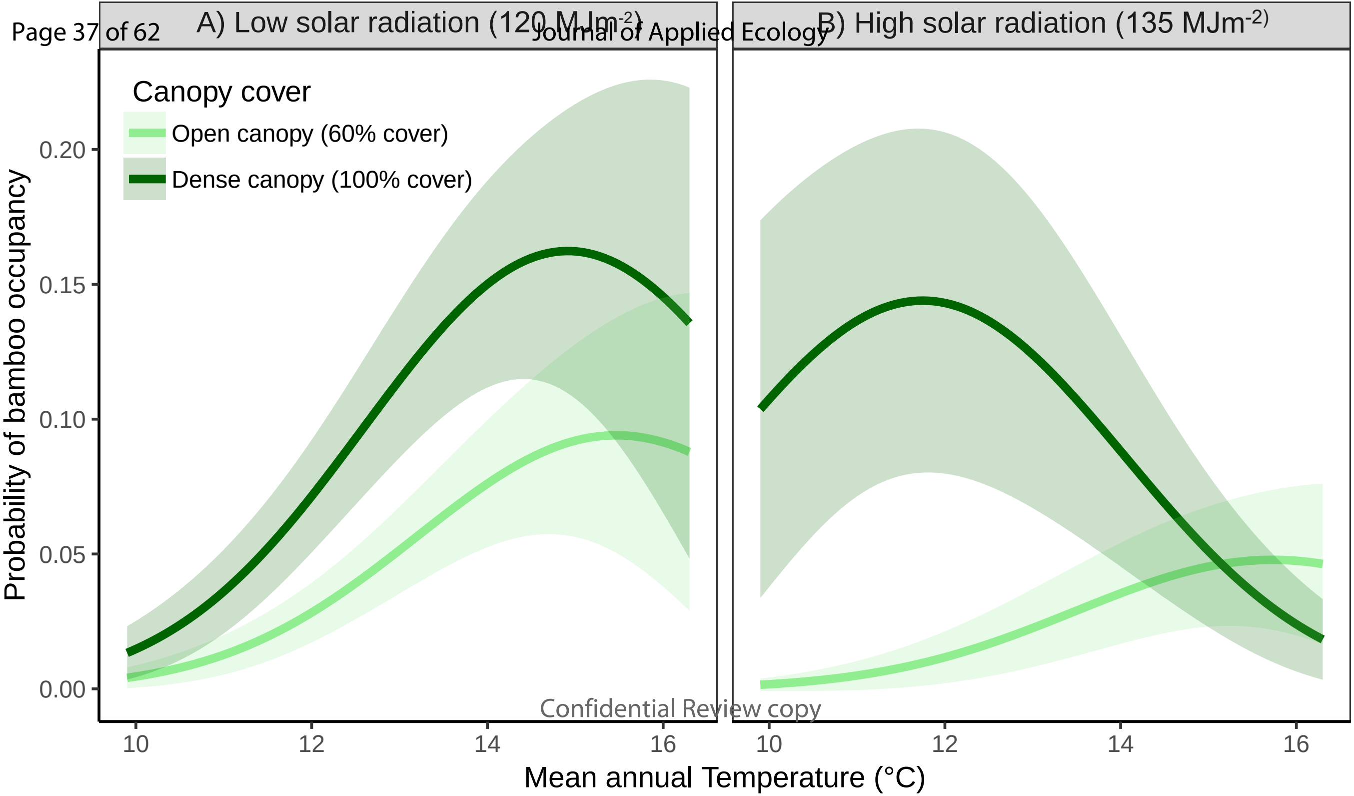

A
Probability of occupancy
0.0
0.2
0.4
1000
1500
2000
2500
Rainfall (mm)
B
Probability of occupancy
0.0
0.2
0.4
0
1
2
3
4
log(Distance to road (km))
C
i) Low solar radiation
ii) High solar radiation
Probability of occupancy
0.0
0.2
0.4
0
10
20
30
40
50
0
10
20
30
40
50
Slope (%)


A) Low solar radiation (120 MJm-2)
B) High solar radiation (135 MJm-2)
Canopy cover
Open canopy (60% cover)
Dense canopy (100% cover)
Probability of bamboo occupancy
0.00
0.05
0.10
0.15
0.20
10
12
14
16
Mean annual Temperature (°C)

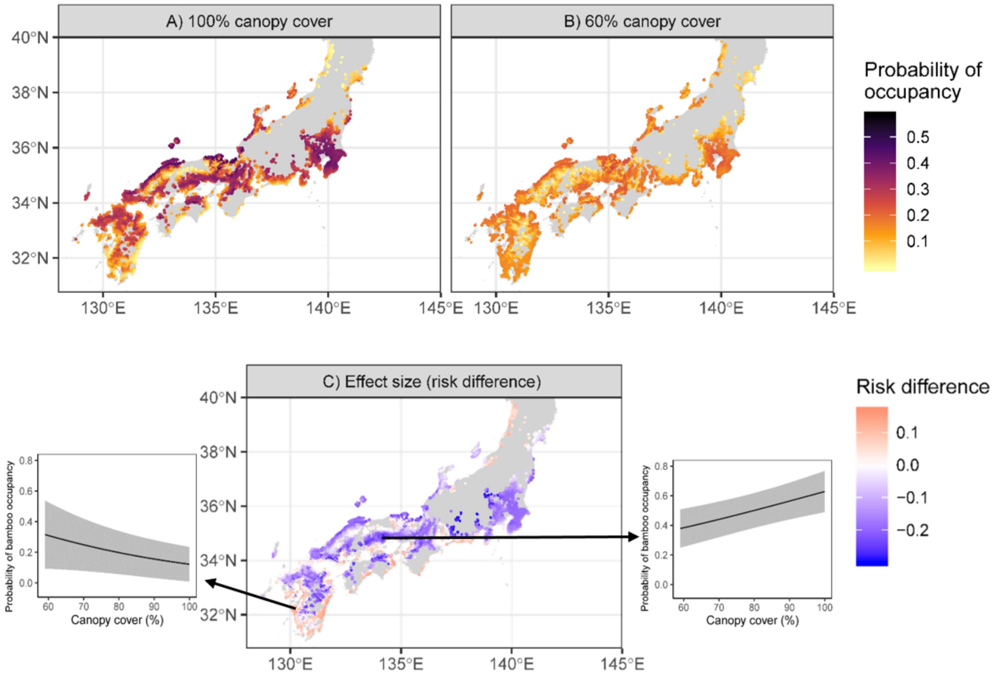


Figure 4. Spatial variation in Phyllostachys bambusoides occupancy, predicted by climate variables solar radiation, mean annual temperature and rainfall, for secondary forests under a) dense canopies (100% cover) and b) more open canopies (60%). C) Spatial variation in the effect of reducing canopy cover from 100% to 60% on predicted bamboo occupancy probabilities (the risk difference, i.e. occupancy difference between A) and B)). Positive values (red) correspond to increases in the probability of bamboo occupancy following a reduction in canopy cover, while negative values (blue) corresponded to a decrease in occupancy probability. Colour shading represents the strength of the effect. Inset are marginal changes in occupancy with canopy cover from two locations differing in solar radiation, rainfall, and temperature. Shown occupancy probabilities are averaged predictions from each model across the top model set (ΔAIC<6), using values of regional climate variables and other covariates held at their median.

Supporting information

Contents

Appendix S1. Review of case studies correlating bamboo expansion with socio-ecological variables in Japan

Previous studies of giant bamboo invasion in Japan have primarily focussed on variation in annual expansion rates of bamboo forests through chronological analyses of aerial photographs or vegetation maps (e.g. Isagi & Torii, 1997; Someya, Takemura, Miyamoto, & Kamada, 2010; Suzuki, 2015; Kobayashi, 2010). Findings from these studies are mixed, with context-dependent effects of key drivers reported. For example, Okutomi et al (1996) found that between 1961 and 1874 in south-western Tokyo, the majority of bamboo invasion was into deciduous broadleaved forest dominated by *Quercus* species (58%), followed by uncultivated fields (17.3%). In Shiga prefecture, Suzuki (2015) found expansion occurred mostly into areas of bushes and grasslands, followed by deciduous broad-leaved forests, and pine forests. Suzuki and Nakagoshi (2008) compared expansion rates at two sites that differed in environmental characteristsics (Table S1.1). Multiple linear regressions at each site revealed differences in the relationship of aerial expansion with a range of explanatory variables at the two sites. In Hiroshima, annual increases in the area of bamboo forest correlated negatively with the proportion of adjacent forest cover (broadleaved forest and conifer plantations), while in cooler Chiba, expansion correlated positively. These differences are suggestive of cross-scale interactions among regional climatic context and local variables. Torii, Okuda, & Atsushi (2005) suggested that sunshine or solar radiation might modify the effects of topography.

Table S1.2 Environmental characteristics of two study sites as described in Suzuki & Nakagoshi (2008)

	Hiroshima	Chiba
Soil	Dry residual immature soils	Brown forest soils
Mean temperature of the coldest month /°C	5.3	3.4°C
Mean temperature warmest month /°C	26.1	24.8
Mean annual temperature/°C	15.0	13.7
Annual precipitation / mm	1187.5	2021.6

While these studies have yielded much insight into key drivers of bamboo expansion locally, their relatively limited geographic extents means that cross-scale interactions have not been characterised, nor understood. This understanding is necessary, however to spatially target the monitoring of secondary forests that are potentially most at risk of invasion, or experiencing the highest levels. Moreover, a primary focus on expansion rates of source bamboo forests has meant that the characteristics of the invaded forests, at different stages of invasion, have been little parameterised, however, secondary forest stand structure and composition are likely to be important determinants of their invasibility (Isagi & Torii, 1997).

Someya et al. (2010) used generalised linear models to predict the occurrance of bamboo forest (pooling all bamboo forest species) within 1-km grid cells across Japan. The climate variables warmth index, annual precipitation, maximum snow depth, in addition to soil type, and land-use type explained variation in bamboo forest occupancy. Takano et al. (2017) examined past (1975–1980) and recent (2012) distributions of bamboo forest (pooling two bamboo forest species) within 1-5-km of 145 weather stations in central and northern Japan. Ecological niche modelling indicated that temperature had a strong influence on bamboo distribution. These studies did not distinguish between bamboo forests established by humans, and those in which bamboo has invaded and become a canopy dominant of planted and secondary forests, therefore provides insight into where bamboo forests have been established by people (i.e. the distribution of ‘satoyama’ landscapes).

Appendix S2. Details of data sources of explanatory variables

Table S2. Data sources of explanatory variables used in this study

Driver	Range within selected plots (units)	Data source and original grain for Japan
Regional-level drivers		
Maximum snow depth	0-365 (cm)	Climate data were 30-year (1971–2000) means, minima and maxima of monthly and annual values within 1-km^2 grid squares across Japan. (Japan Meteorological Agency, 2010). https://www.jma.go.jp/jma/indexe.html
Solar radiation	113 – 147Jm^{-2}	
Temperature	6.3 – 18.8°C	
Rainfall	936.7 – 3699.3 (mm)	
Landscape-level drivers		
Distance to forest edge	0 – 933.7 (m)	Fifth Basic Survey on Natural Environment Conservation (surveyed in 1994–1998 with a scale of 1:50,000 provided as vector data) by the Ministry of the Environment of Japan (http://gis.biodic.go.jp/webgis/sc-023.html).
Distance to road	0 – 60.9 (km)	Road map obtained from the Geospatial Information Authority of Japan (GSI) Global Map Japan version 2.2 (http://www.gsi.go.jp/kankyochiri/gm_japan_e.html)
Local-level drivers		
Slope inclination	0-56.3 (%)	Derived from 30-m resolution global digital elevation model (DEM) derived from GTOPO30. Northness and eastness were calculated as the cosine and sine, respectively, of slope aspect. Topographic position index was calculated as the difference between elevation at the site, and the mean elevation within a 100-m radius.
Eastness	-1 – 1	
Northness	-1 – 1	
Canopy cover	30-100 (%)	Ministry of Environment's 'Natural Environment Information GIS' dataset (http://www.biodic.go.jp/chm/). Forest type was classified according to the species recorded as the canopy dominant.

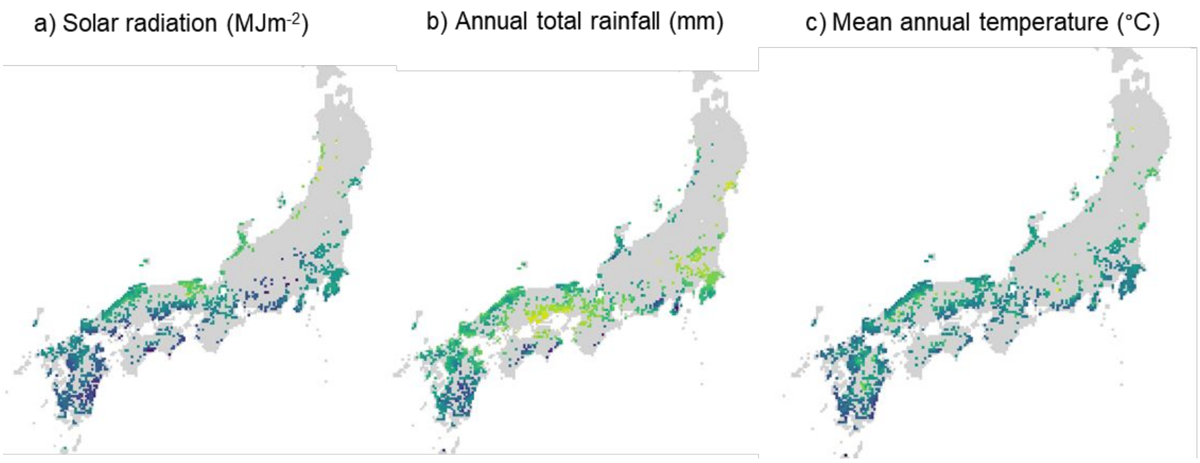


Figure S2.1. Regional variation in climatic variables (high=dark; low=light). Only pixels within 1-km of bamboo forest are mapped (see appendix S3 for explanation).

Figure S2.2 Typical managed satoyama landscape from Shiga prefecture, comprising mosaics of paddy fields, settlements, secondary forests and bamboo forests. Photo: R Spake.

Appendix S3. Details of plot stratification from the Ministry of Environment's 'Natural Environment GIS' dataset.

The vegetation data were accessed and downloaded from The Biodiversity Center of Japan (Biodic-J) in May 2018.

Distinguishing forest at risk of invasion

Large vegetation databases that can contain plot data from heterogeneous sources (Michalcova *et al.*, 2011) require appropriate data stratifications prior to analyses (Pysek & Chytry, 2014), and cautious interpretation with respect to potential biases incurred, for example, from under/over-representation of particular habitat types (Michalcova *et al.*, 2011). We therefore note here that our interpretation of the results will focus on the trends in the relationship between bamboo occupancy and environmental variables, rather than the actual estimated probabilities.

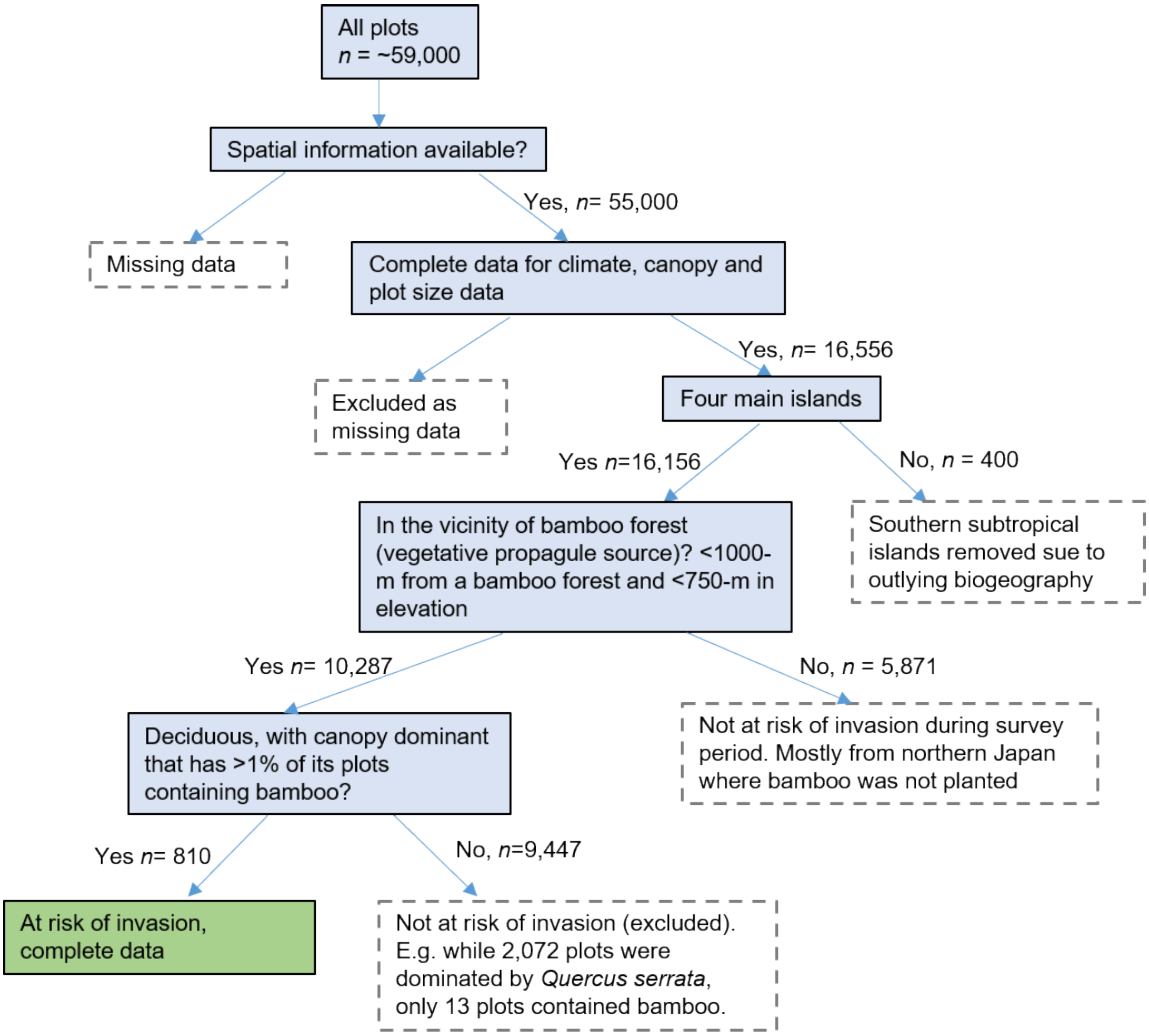


Figure S3.1. Selection procedure applied to ~59,000 data plots held by the Ministry of Environment, according to data availability and plausible invasion risk.

From the vegetation database, we took plots which had complete data available for spatial coordinates, climate variables, canopy dominant species and canopy cover (*n* = 16,556; Figure S3.1).

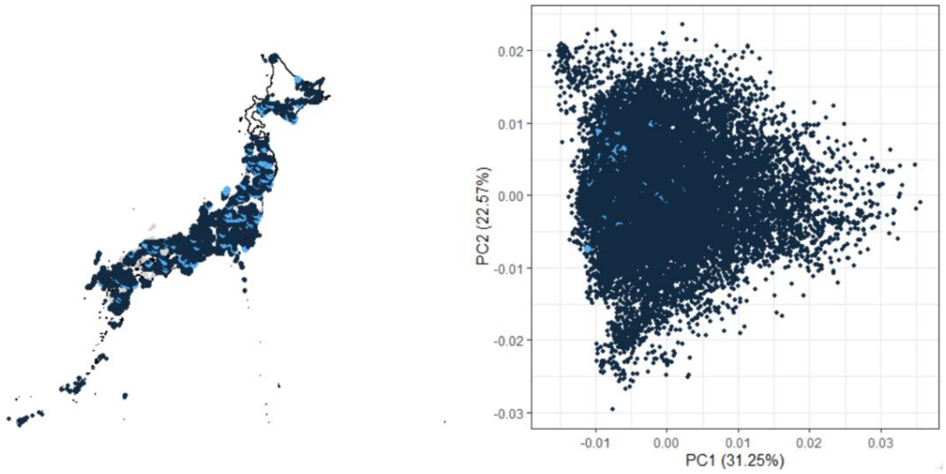


Figure S3.1. Distribution of all plots with complete data in geographic (left) and environmental (right) space. Bamboo presences and absences are shown in light and dark blue, respectively. The environmental space comprises the first principal components derived from a PCA of standardised environmental variables: solar, temperature, rainfall, slope, canopy cover.

Next, we excluded plots from the southern subtropical islands due a low sample size of plots occurring at outlying temperature values, and differences in management in these regions (*n* = 16,156; Figure S3.2).

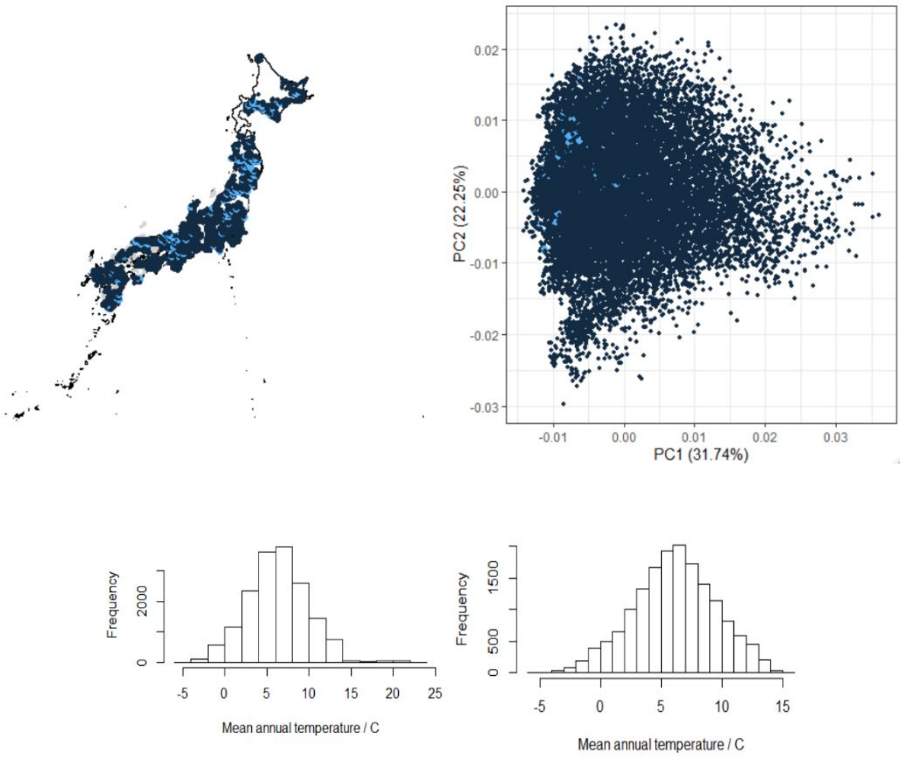


Figure S3.2. Distribution of plots in geographic (left) and environmental (right) space, after excluding islands. Bamboo presences and absences are shown in light and dark blue, respectively. The environmental space comprises the first principal components derived from a PCA of standardised environmental variables: solar, temperature, rainfall, slope, canopy cover. Bottom: Relative frequencies of plots according to mean annual temperature values before (left) and after (right) removal of subtropical islands.

Next, we selected plots that were plausibly at risk. The susceptibility of an ecosystem to invasion depends on propagule pressure, abiotic conditions and biotic interactions (Catford *et al.*, 2009). We stratified the available plots according to these three parameters to identify forests potentially at risk of invasion.

Stratifying by propagule pressure

Not all of the 16,156 plots were at risk of invasion by bamboo during the survey period (2000-2015). For example, bamboo forests (vegetative propagule sources) were planted predominantly across central and western Japan, therefore plots in northern Japan were not at risk of invasion during the survey period (although may be in the future; Takano et al. 2017). Firstly, we considered plots at risk if they were close to planted bamboo forest (vegetative propagule sources), according to distance and elevation. To identify such plots, we used a digital elevation map and a land cover map that distinguished bamboo forests (The 5th Basic Survey of Natural Environment Conservation by the Ministry of Environment of Japan; http://www.biodic.go.jp/trialSystem/shpddl.html). Bamboo has been shown to spread at a maximal rate of 8-m per year in Japan (Torii & Okuda, 2010). Over 18 years (between the release of the vegetation map and the last plot survey), bamboo could have maximally spread 8×18 = 144-m from the bamboo forests. However, plots farther than this distance from a planted bamboo forest contained bamboo (Figure S3.3). The available land cover map distinguishes land units of at least 0.25-ha, i.e. only relatively large bamboo forests. We assumed that if large bamboo forests were planted, then smaller, unmapped forests were likely also present in the vicinity. We therefore considered plots within a distance of 1000-m of mapped bamboo forests to be ‘at risk’ of invasion, as 99% of plots containing bamboo were within 1000-m. Plot elevation ranged between 0 and 2735-m. We selected all plots below an elevation of 750-m, to identify plots near to residential areas, i.e. at elevations below which bamboo forests were extensively planted (Fukamachi *et al.*, 2001). 99% of plots containing bamboo were below 750-m. This initial selection on propagule pressure yielded 10,287 plots (Figure S3.3).

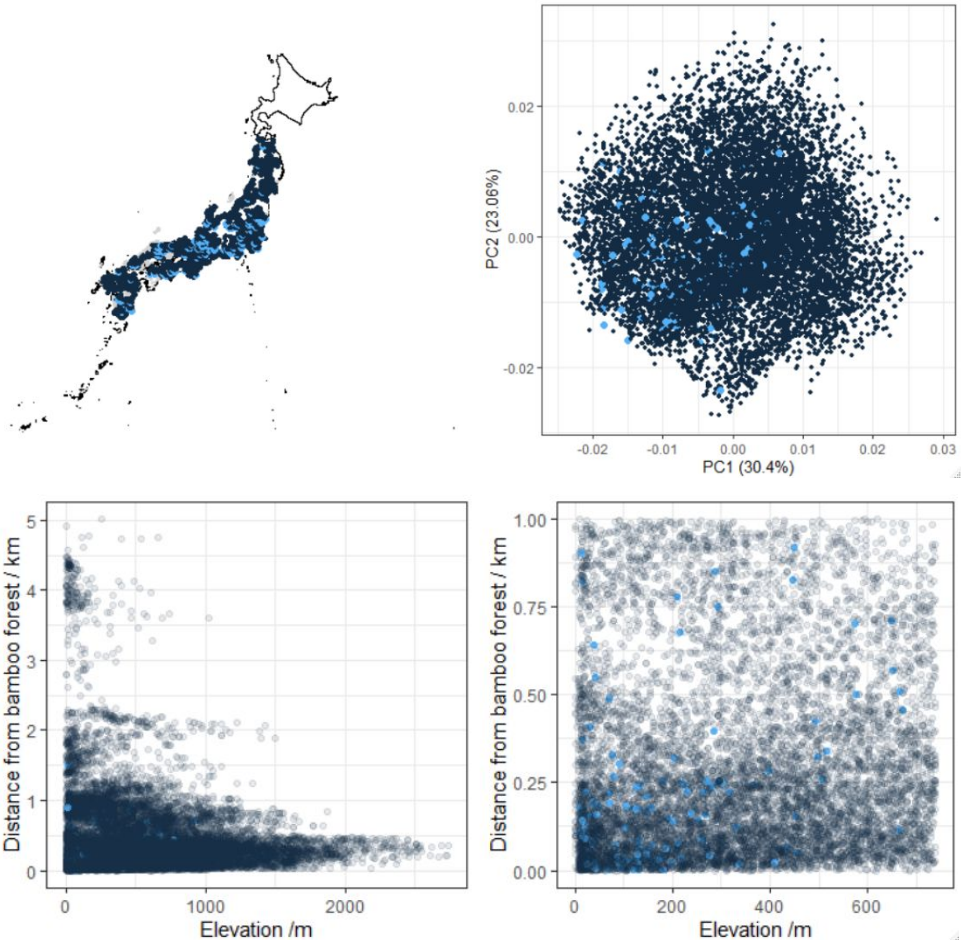


Figure S3.3. Top: Distribution of plots in geographic (left) and environmental (right) space after stratification by propagule pressure. The environmental space comprises the first principal components derived from a PCA of standardised environmental variables: solar, temperature, rainfall, slope, canopy cover. Bottom: Distribution of selected plots according to elevation and distance from bamboo forest, before (left) and after (right) stratification by propagule pressure. Bamboo presences and absences are shown in light and dark blue, respectively.

Stratifying by abiotic characteristics

The environmental characteristics of a site must be hospitable for invasion to occur (Catford *et al.*, 2009), so we selected plots with abiotic characteristics within the hospitable range of bamboo. First, we selected only deciduous plots that were dominated by tree species with at least 1% of their plots containing bamboo. Deciduous species were identified by matching the canopy dominant with the phenology type (deciduous/evergreen) of the TRY database (Kattge *et al.*, 2019). Deciduous plots only were selected to limit covariation between temperature and phenology type in Japan (Kira, 1991; Suzuki *et al.*, 2015), which in turn could modify the effect of canopy cover on invasibility (*n* = 5,906; Figure S3.4). Selecting plots dominated by tree species within which bamboo was present in >1% of plots (Figure S3.5), stratifies plots so that the sampled forest types, and their microclimates and management regimes that are potentially invasible. (*n* = 1,017 Figure S3.4, bottom).

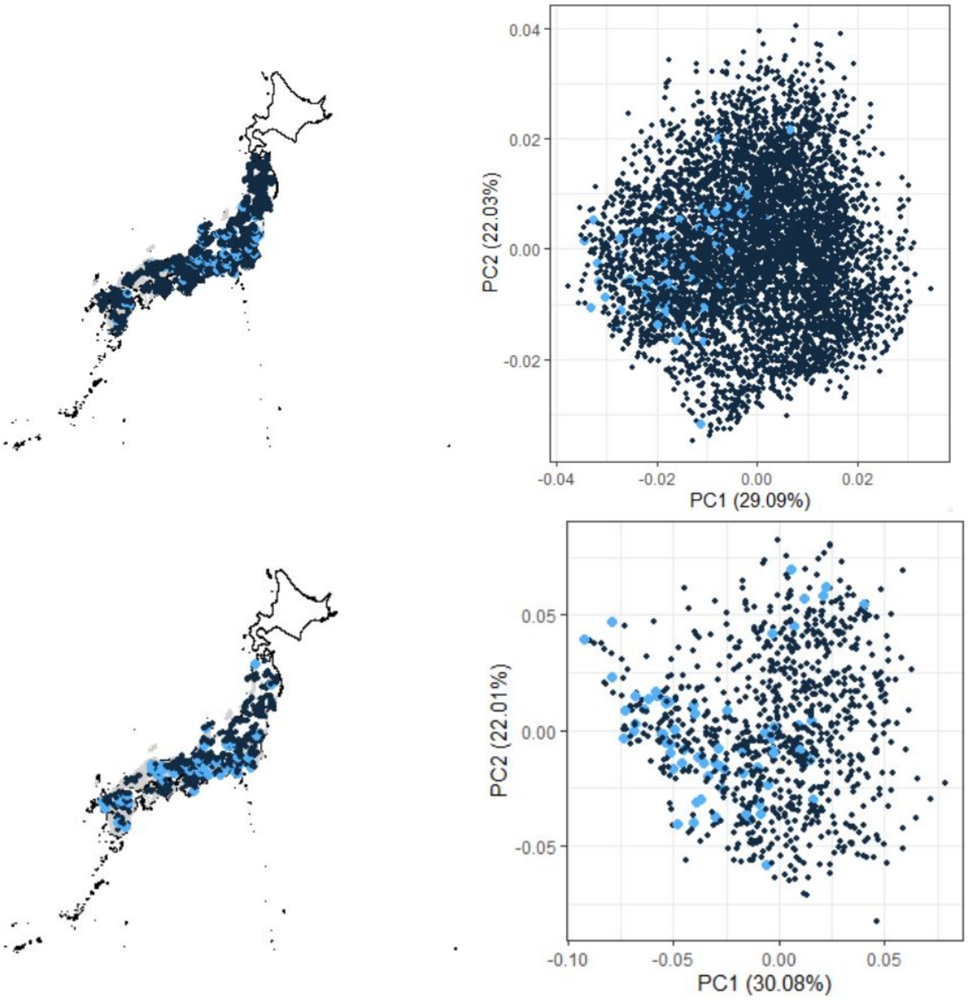


Figure S2.4. Distribution of plots in geographic (left) and environmental (right) space after exclusion of plots dominated by evergreen tree species (top), and deciduous species within which 99% of plots did not contain bamboo (bottom). Bamboo presences and absences are shown in light and dark blue, respectively. The environmental space comprises the first principal components derived from a PCA of standardised environmental variables: solar, temperature, rainfall, slope, canopy cover.

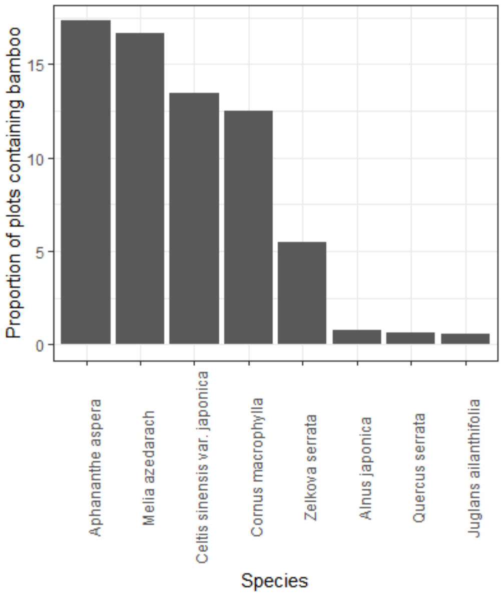


Figure S3.5 Proportion of plots that contained bamboo by tree species.

Next, we stratified plots based on the range of abiotic variables observed within plots where bamboo was present. We did this by selecting plots that occurred within the variable ranges of plots that contained bamboo for mean annual temperature, rainfall, and solar radiation. This stratification by abiotic variables yielded $n = 810$ plots (Figure S3.6)

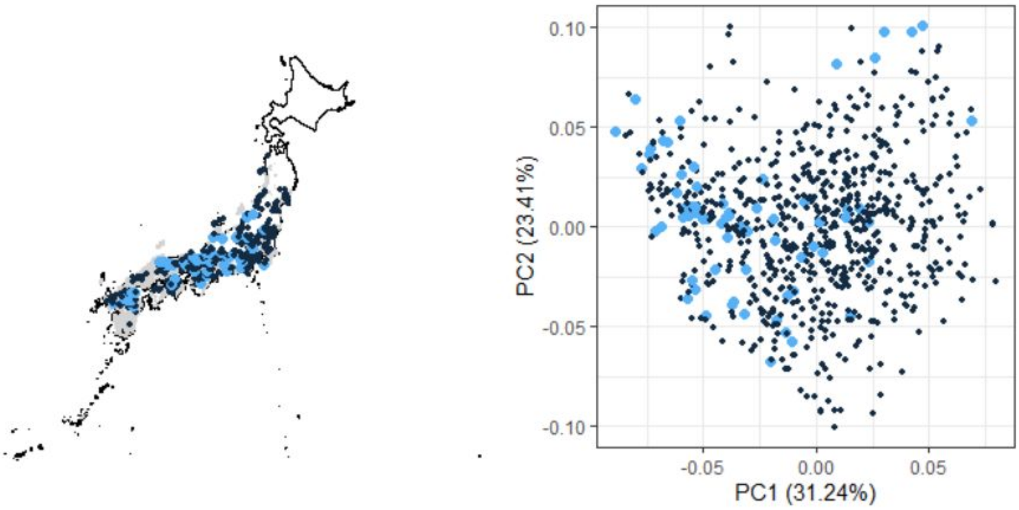


Figure S3.6. Distribution of plots in geographic (left) and environmental (right) space after stratification by abiotic characteristics. Bamboo presences and absences are shown in light and dark blue, respectively. The environmental space comprises the first principal components derived from a PCA of standardised environmental variables: solar, temperature, rainfall, slope, canopy cover.

Appendix S4. Details of data exploration prior to statistical modelling of bamboo invasion

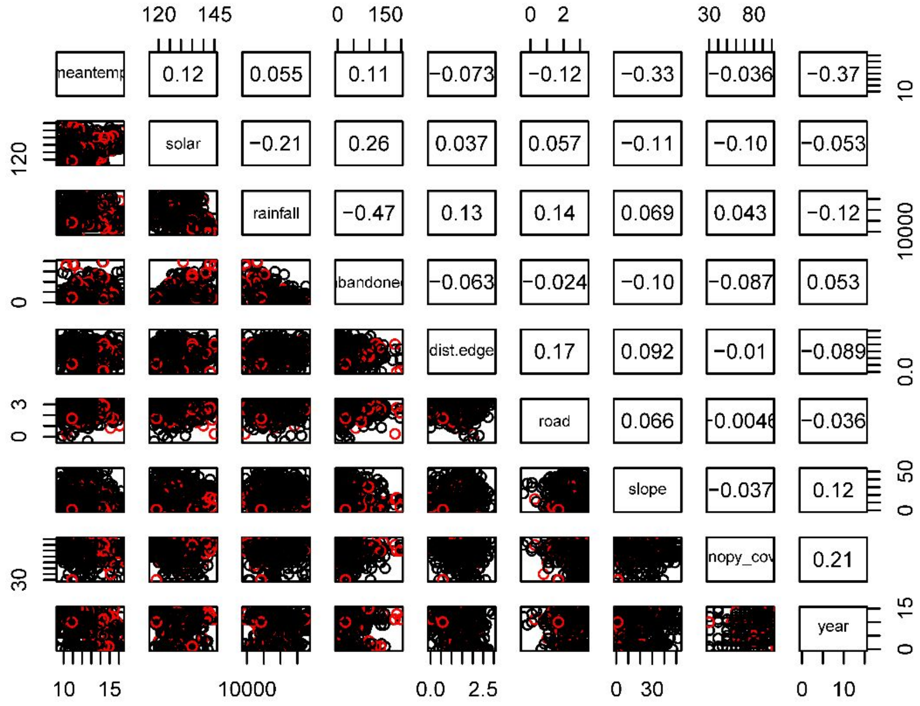


Figure S.3.1. Spearman's rank correlation coefficients of explanatory variables used to model giant bamboo occupancy. Sites values are plotted in red and black to denote presence and absence of bamboo, respectively.

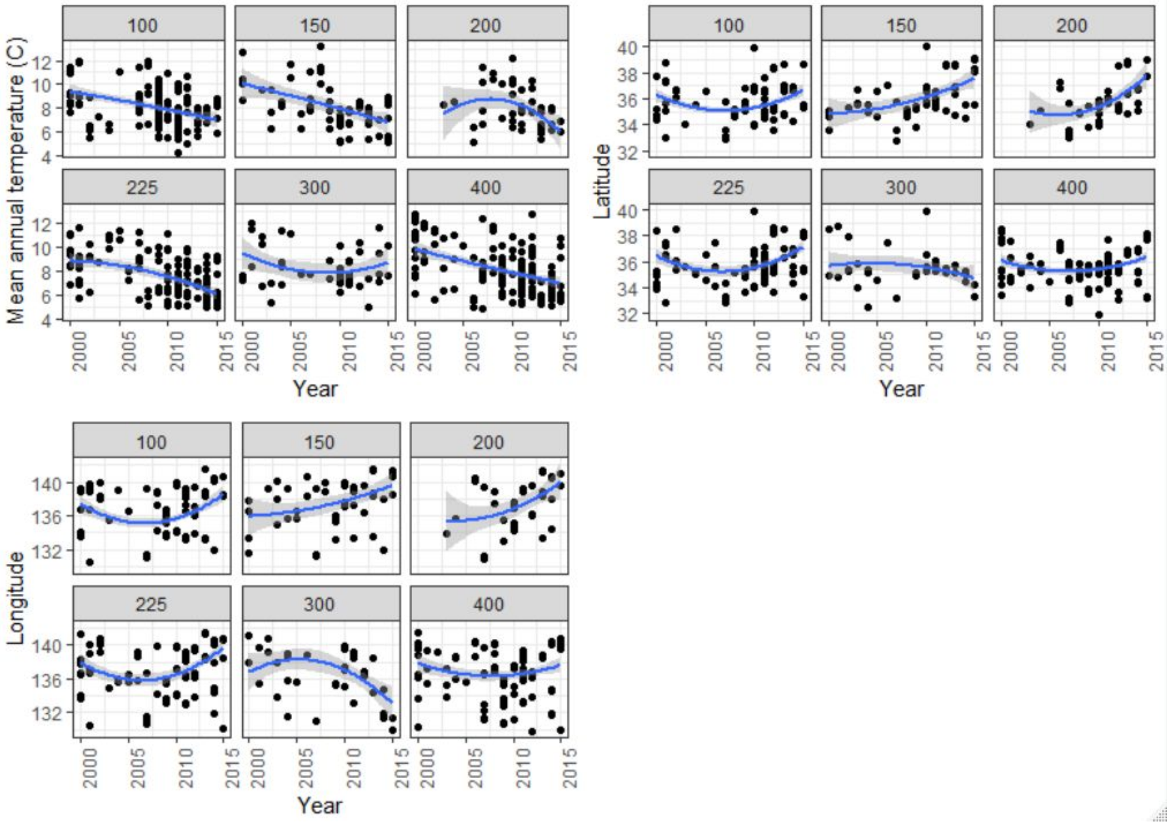


Figure S3.1. Covariation between sampling year and temperature as well as spatial variables latitude and longitude. Shown are relationships for the six most common plot sizes (panel names, in m²). Non-parametric smooth curves were computed by locally estimated scatterplot smoothing. The trends suggest that across the years, vegetation surveys were conducted progressively over space.

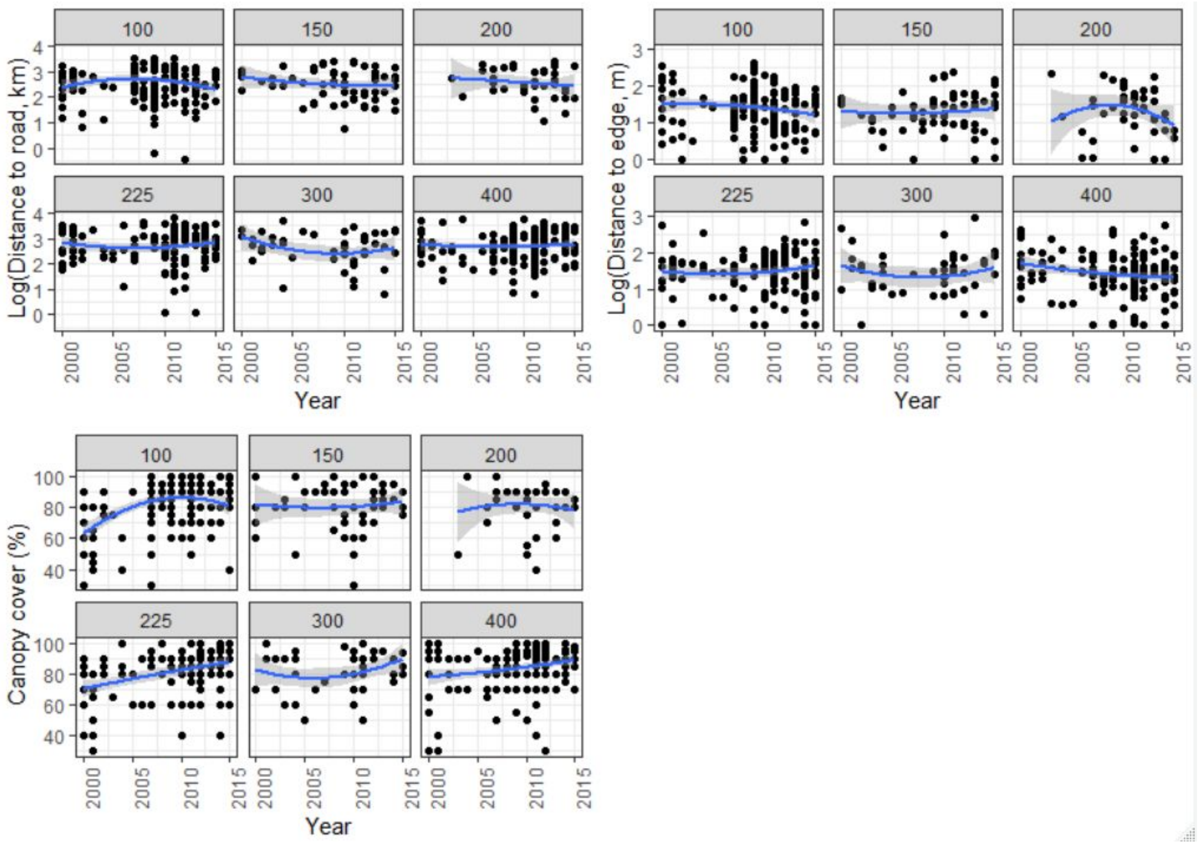


Figure S4.3. Covariation between sampling year and local variables distance to road, distance to edge and canopy cover. Shown are relationships for the six most common plot sizes, suggestive that they were collected as part of the same monitoring scheme. Non-parametric smooth curves were computed by locally estimated scatterplot smoothing. No trends are apparent.

Bamboo cover-abundance data were available for a small subset (21) of the forest plots. There was no relationship between canopy and bamboo cover-abundance (Spearman’s *rho* = -0.14), indicating that canopy cover does not represent the cover of bamboo within the forest stands.

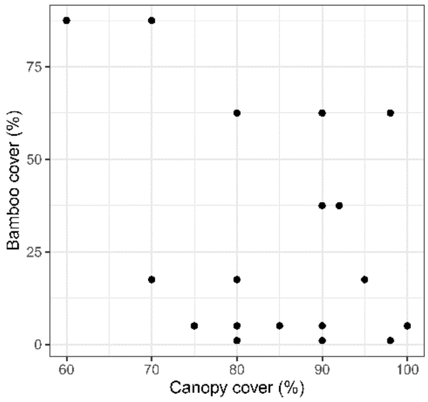


Figure S4.4 Covariation between canopy and bamboo cover, for plots with available bamboo cover data.

Appendix S5. Details of modelling variation in bamboo (*Phyllostachys bambusoides*) occupancy

Model set generation and comparison was done in two stages. While we had formulated *a priori* hypotheses, the first stage was exploratory (Symonds & Moussalli, 2011), intended to ascertain i) how temperature should be summarised, i.e. as averages of annual means, minima or maxima, ii) whether to include non-linear forms of temperature, i.e. whether polynomials improve model fit (Fisher *et al.*, 2018), and iii) whether models containing the interactions that represent the hypothesised biological mechanism were supported by the data (Bolker, 2008). The objective of the second stage was to conduct multi-model inference.

Stage 1: Exploration

Global models consisted of the following variables:

Bamboo (0/1) ~ rainfall + snow depth + distance to forest edge + distance to road + eastness + northness + solar*canopy cover*temperature + solar*slope + offset(log(plot size))

Temperature variables were substituted as follows:

Linear and quadratic functions of temperature.

The temperature variable was either 30-year (1971–2000) means, minima and maxima of annual values.

By constructing and comparing models with a specific interaction among variables, that corresponded to an *a priori* hypothesis, we distinguish our testing of rigorous hypotheses from a 'fishing expedition' that seeks significant predictors among a large group of contenders and all of their possible second or third order interactions (Burnham & Anderson, 2002). This initial exploratory stage showed that that the interactions consistently appeared in highly supported models (ΔAIC<1), in addition to both a linear and quadratic term for mean annual temperature.

Multi-model inference is nonsensical when averaging over models in which interaction and polynomial terms are both present and absent, because the magnitude and sign of coefficients can vary widely across these models (Cade, 2015). We therefore restricted our global model set to models containing the interactions and second order polynomial of mean annual temperature. This was further justified because: i) we were interested in the particular biological mechanism underpinning these interactions, and multi-model inference places a strong emphasis on *a priori* formulation of hypotheses (Harrison *et al.*, 2017), and ii) these terms were supported by the data (Bolker, 2008). Moreover, restricting the candidate model set avoids the problem of comparing 'too many models' (Burnham & Anderson, 2002), that could potentially include spurious or biologically implausible models (Grueber *et al.*, 2011).

Step 2: Multi-model inference

We aimed to produce predictions that incorporate uncertainty averaging across all model predictions in the top model set the parameter estimate of a model by that model's Akaike weight (Symonds & Moussalli, 2011). Model averaging requires the identification of a 'top model set' containing all models with comparable support in the data, typically according to the ΔAIC relative to the minimum adequate model with the lowest AIC. Different cut-offs have been proposed to define the top model set. We delineated the top model set as containing models with ΔAIC<6 (Richards, 2005, 2008; Harrison *et al.*, 2017). Averaging was deemed sensible, because the parameter estimates for the predictor variables did not vary widely in magnitude, and never in sign across models (Table S6.1).

We applied natural model averaging of parameter estimates for each predictor, averaged only over models in which that predictor appeared, weighted by the summed weights of those models (Grueber *et al.*, 2011). Natural averaging was done instead of zero averaging, where parameter estimates (and errors) of zero are substituted into models where the given parameter is absent, because our aim was not to rank the importance of predictor variables (Nakagawa & Freckleton, 2010), but to model biologically meaningful responses.

To visualise variation in predicted probabilities of bamboo occupancy with the predictor variables, we used the predict.glm() function to generate predictions for each model in the top model set. Following Cade (2015), we averaged the predicted occupancy values across each model.

Appendix S6. Results of multi-model inference

Table S6.1 Parsimonious generalised linear models of secondary forest invasion by bamboo. Models with considerable support are shown, with ΔAIC<10, ranked by AIC weight (Burnham and Anderson, 2004). The top model set was defined by containing models with ΔAIC<6 (Richards, 2005, 2008; Harrison *et al.*, 2017). Shown are the standardised regression coefficients for each term (column) in each models (rows). The goodness of fit of these models (pseudo-R^2) was calculated following Nagelkerke (1991).

intercept	canopy cover	dist.edge	dist.road	rainfall	slope	solar	temp	$temp^2$	canopy cover:solar	canopy cover:temp	slope:solar	solar:temp	canopy cover:solar:temp	*K*	AIC	delta	weight	R^2
-2.968	0.396		-0.324	-0.232	-0.790	-0.190	0.901	-0.262	0.373	-0.104	-0.237	-0.279	-0.292	13	395.253	0.000	0.372	0.24
-2.961	0.360		-0.341		-0.819	-0.116	0.880	-0.242	0.358	-0.077	-0.226	-0.303	-0.290	12	395.800	0.548	0.283	0.23
-2.969	0.395	-0.008	-0.324	-0.231	-0.790	-0.189	0.900	-0.261	0.372	-0.103	-0.237	-0.279	-0.291	14	397.248	1.996	0.137	0.24
-2.963	0.358	-0.028	-0.341		-0.817	-0.113	0.877	-0.241	0.353	-0.075	-0.224	-0.302	-0.288	13	397.745	2.493	0.107	0.22
-2.910	0.370			-0.266	-0.806	-0.220	0.921	-0.261	0.377	-0.064	-0.250	-0.308	-0.309	12	399.284	4.031	0.050	0.21
-2.908	0.332				-0.839	-0.147	0.898	-0.233	0.359	-0.031	-0.241	-0.337	-0.311	11	400.715	5.462	0.024	0.21
-2.911	0.367	-0.022		-0.263	-0.804	-0.216	0.918	-0.259	0.373	-0.062	-0.247	-0.308	-0.307	13	401.251	5.998	0.019	0.22
-2.910	0.327	-0.048			-0.834	-0.141	0.893	-0.231	0.350	-0.027	-0.236	-0.335	-0.307	12	402.555	7.302	0.010	0.21

Table S4.1. Parameter estimates of the averaged model that explained bamboo occupancy. Variables were centred and scaled prior to modelling.

Term	Estimate	S.D.
Intercept	-2.960	0.218
canopy cover	0.378	0.203
dist.road	-0.332	0.126
dist.edge	-0.017	0.122
rainfall	-0.236	0.149
slope	-0.803	0.185
solar	-0.161	0.202
temp	0.894	0.234
$temp^2$	-0.253	0.144
canopy cover:solar	0.366	0.190
canopy cover:temp	-0.088	0.165
solar:temp	-0.292	0.139
slope:solar	-0.233	0.173
canopy cover:solar:temp	-0.292	0.124

Appendix S7. Model validation

Following Zuur & Ieno (2016) standardized residuals were plotted against each covariate, each covariate not in the model, and against time (year) and space variables (latitude and longitude). Residuals were estimated using the DHARMa package for each model in the top model set (Hartig, 2018).

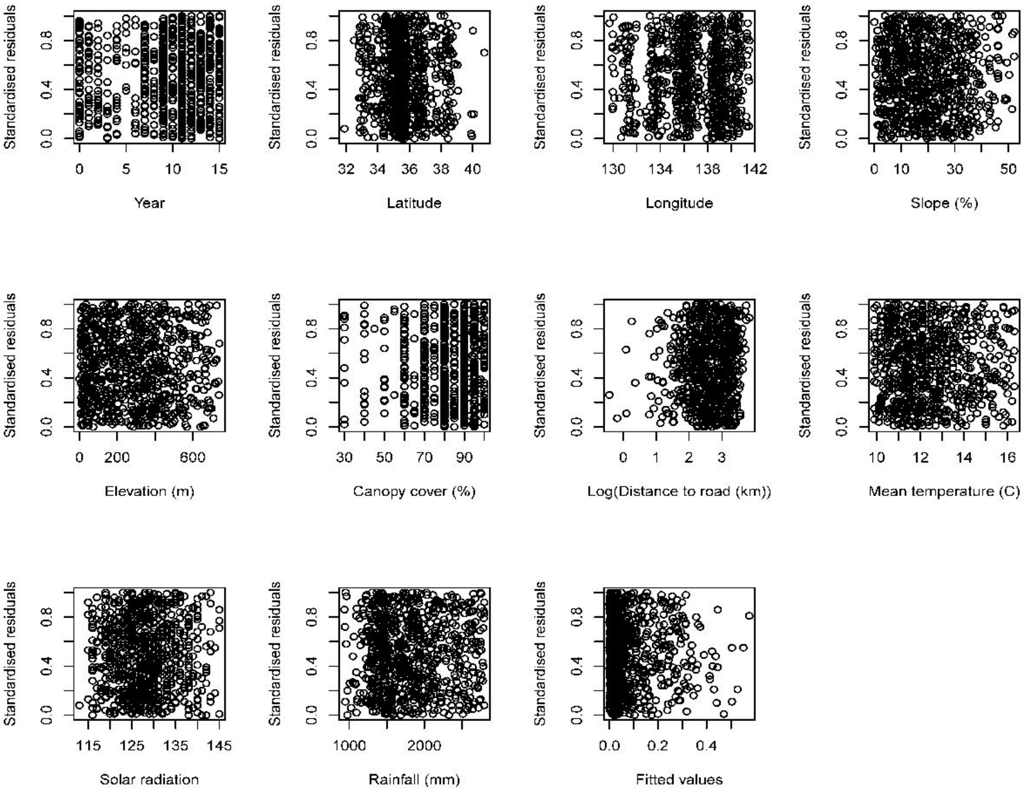


Figure S7.1. Absence of residual patterns for the fullest model, containing all predictors) in the top model set.

Generalised variance inflation factors GIF$^{(1/(2\times\mathrm{df}))}$ were computed following Fox & Monette (1992). All values are <2, suggesting collinearity is not an issue.

Table S7.1. Generalised variance inflation factors for terms contained within the fullest model, calculated following Fox & Monette (1992).

Term	GVIF$^{(1/(2\times\mathrm{df}))}$
canopy cover	1.53
slope	1.11
solar	1.67
temperature	1.88
temperature^2	1.81
distance to road	1.02
rainfall	1.09
distance to edge	1.02
canopy cover:temperature	1.78
canopy cover:solar	1.56
solar:temperature	1.38
slope:solar	1.44
canopy cover:solar:temperature	1.51

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