Title: Comparison of six methods for stabilizing metapopulation dynamics and for their robustness against census noise

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ABSTRACT

Natural populations often encounter heightened risks of extinction due to mismatches between their inherent traits and the ecological contexts they inhabit. These risks amplify with the ongoing degradation of wild habitats and climatic shifts. Recognizing that not all populations can prevent extinction independently, several methods have been theoretically proposed to protect vulnerable populations using external interventions. Yet, these methods are under-explored in spatially structured populations, or metapopulations, and remain untested in the presence of potential census inaccuracies. In this study, we assessed six population stability methods, previously validated in isolated populations, comparing their efficacy in metapopulations, using comprehensive biologically realistic simulations. We employed a recognized composite index to compare the performance of the population stability methods based on their stability outcomes and associated implementation costs. Our evaluations encompassed a range of ecological conditions, factoring in population growth rate, capacity, and migration patterns, inclusive of both symmetric and asymmetric migration. Without external interventions, we observed unique dynamics across these conditions, each with differing extinction susceptibilities. Remarkably, to decrease extinction probabilities to a specified threshold, the Adaptive Limiter Control method was consistently superior irrespective of the original dynamics. Conversely, for curbing population size fluctuations, the Lower Limiter Control emerged as the most potent, trailed closely by the Adaptive Limiter Control and Both Limiter Control methods. Importantly, these method rankings remained consistent even amidst varying census uncertainties. Our results offer a foundation for developing policies and conservation strategies with specific actionable recommendations, particularly in the management of natural populations facing extinction risks.

Key words

Constancy, persistence, effective population size, effort of implementation, spatially-structured populations

1. Introduction

Complex temporal fluctuations in population size are a ubiquitous phenomenon in nature (Lundberg et al. 2000; Clark and Luis 2020). While external environmental factors are known to induce such fluctuations (Borowsky 1971), it's the intricate interplay between the life-history of resident populations and local environmental conditions that ultimately shapes these temporal dynamics (Gamelon et al. 2017; Tung et al. 2019). Over time, some populations may exhibit diminishing magnitudes of fluctuation, harmonizing their life-histories with environmental cues, but not all populations demonstrate such resilience. If these fluctuations intensify or sustain at elevated levels, populations can undergo frequent declines, amplifying their risk of extinction (Escudero et al. 2004; Smith and Meerson 2016). Hence, devising strategies to stabilize these vulnerable populations has been at the forefront of research for ecologists, conservation biologists, and biological population managers for many years.

In the past three decades, theoretical propositions have introduced several methods to stabilize such inherently extinction-prone populations (McCallum 1992a; Corron et al. 2000; Hilker and Westerhoff 2005; Dattani et al. 2011; Sah et al. 2013a; Tung et al. 2014). These methods, commonly referred to as population control or stability methods, primarily operate by modulating population size — either by externally adding individuals or strategically removing them based on current census size. Their practical applicability is a key advantage, allowing deployment in actual biological populations without exhaustive knowledge of the underlying dynamics or system parameters, which is in contrast to the chaos-control methods proposed to stabilize chaotic non-linear dynamics earlier (Andrievskii and Fradkov 2003; Fradkov and Evans 2005). Despite these advantages, the widespread adoption of population stability methods in conservation has been limited. One major factor for this reluctance stems from the observation that, with a couple of exceptions (Dey and Joshi 2013; Sah et al. 2013a), most methods have been explored solely in case of single, isolated populations (Corron et al. 2000; Hilker and Westerhoff 2005; Dattani et al. 2011; Tung et al. 2014).

However, in natural settings, populations are seldom isolated. Organisms of a species typically do not occupy a shared space or pool resources uniformly. Instead, more commonly, groups of individuals of a species inhabit distinct, spatially dispersed habitats. Should these habitats fall within an organism's range of movement, migration or dispersal (used interchangeably here) becomes commonplace. These networks of spatially distributed populations, interconnected by such migrations, are termed spatially structured populations or 'metapopulations'. Insights from studying population stability methods in single isolated populations prove inadequate for understanding metapopulation dynamics. This is primarily because, migration within a metapopulation between the constituent subpopulations plays a major role in shaping the dynamics and stability of metapopulations (Gyllenberg et al. 1993; Stacey et al. 1997; Hanski 1998; Dey and Joshi 2006).

Migration modalities, driven by factors such as food foraging, mate-seeking, or habitat preference, and shaped by the connectivity and migratory tendencies of local populations, play a crucial role in population dynamics. From a population dynamic perspective, emigration can alleviate resource competition within a subpopulation, while immigration can exacerbate it, increasing vulnerability to extinction. On the other hand, immigration can rejuvenate a locally extinct population, eliminating the need for external intervention. Therefore, the migration intricately influences local dynamics and, by extension, overall metapopulation fluctuations (Gyllenberg et al. 1993; Stacey et al. 1997). Prior research has shown that both low and high migration rates can differentially modulate metapopulation stability, even under uniform environmental conditions across subpopulations (Dey and Joshi 2006). Thus, extrapolating findings from spatially unstructured populations to metapopulations becomes inadequate.

In this context, our study introduces a simulation framework to explore performance of six stability methods (mathematical formulations in Table S1) in metapopulations consisting of two subpopulations connected via migration with varying characteristics. By introducing combinations of intrinsic growth rate and carrying capacity parameters, we have constructed diverse ecological scenarios (exact descriptions in Table S2) to evaluate the efficacy of the population stability methods through biologically realistic simulations. For this comparison, we used an established statistic (following Tung et al. 2014) that combines measures of various aspects of population stability with the costs associated with the implementation of the stability methods. Furthermore, we assessed the relative performance of these population stability strategies in the presence of three distinct census inaccuracies: white noise, overestimation, and underestimation—a pertinent aspect that has often been overlooked (Supplementary section 4).

2. Materials and Methods

2.1. Spatial structuring and population growth model

We adopted a metapopulation framework comprising two subpopulations interconnected through migration. For our study, all metapopulations were treated as homogeneous, ensuring identical environmental conditions across both subpopulations. Various migration rates and environmental characteristics differentiated our treatment groups (refer to Table S2). We used a popular population growth model, Ricker map (Ricker 1954), to model the dynamics of each subpopulation. Mathematically this map is given as $N_{t+1} = N_t \exp(r(1-N_t/K))$; where r, K and N_t denote intrinsic growth rate, carrying capacity and population size at time t, respectively. The popularity of this model stems from its intuitive formulation (May and Oster 1976), and the fact that it can be derived from the first principles as long as the individuals of the concerned population are distributed randomly over space and undergoing scramble competition (Brännström and Sumpter 2005). As these properties are rather common in biology, Ricker map has been implemented to capture empirical dynamics of species across diverse taxa, including bacteria (Ponciano et al. 2005), fungi (Ives et al. 2004), ciliates (Fryxell et al. 2005), insects (Dey and Joshi 2006) and fishes (Ricker 1954). Thus, outcomes of simulations utilizing this model are anticipated to be broadly generalizable.

2.2. Replications, initial conditions and reset

In order to obtain a generalizable output, we considered 70 replicates for each treatment group, and thus all demographic or population dynamic matrices in the figures were presented as average (±SEM) over all these replicates. At the beginning, time-series for all replicates in all the treatment groups were initiated with 20 individuals in each subpopulation. Whenever population size of the entire metapopulation became zero, we reset population size of each of the subpopulations to eight (following Dey and Joshi 2006).

2.3. Biologically realistic assumptions

We incorporated a number of biologically realistic features in our simulations. Firstly, in order to account for the fact that organisms come in whole numbers, we rounded off all outputs of the Ricker model, the number of migrants and the number of individuals to be introduced to or removed from the system as prescribed by the control methods, to their nearest integer values. Secondly, empirically obtained timeseries are typically short and it is rarely possible to exclude transients from them prior to analysis. In order to keep a parity with that, we decided to consider the transients in our study by restricting our analysis for the first 50 generations of population growth time-series, instead of studying the steady states of a system. Thirdly, stochastic noise is ubiquitous in any quantitative aspect of biology and it is known that disregarding this noise may have significant impact on, *inter alia*, the outcome of theoretical studies involving stabilizing populations through external perturbations (Dey and Joshi 2007). To reflect this, we introduced noise in the growth rate and carrying capacity values for each subpopulation at each iteration. A number was picked using a uniform random number generator from U(-0.2, 0.2), and added to the regime-specific value of r as suggested by the Table S2. Similarly, the value of carrying capacity was picked using the uniform random number generator from U($0.9 \times K$, $1.1 \times K$), where K is the regime-specific value of carrying capacity. The values of the noise are at par with the previous studies on extinction prone populations (Tung et al. 2014). Fourthly, whenever population size becomes very low, the risk of extinction in the next generation increases significantly due to various reasons including stochastic death of the breeding individuals, or all breeding individuals being of same sex. We implemented this possibility of stochastic extinction by assuming that there is 50% chance of extinction if subpopulation size goes below 4 (following Dey and Joshi 2006; Tung et al. 2014).

2.4. Measures of stability and synchrony in unperturbed populations

Prior to comparing the control methods, we first studied the dynamics of the unperturbed populations of all the twelve metapopulation regimes. For this, we measured two aspects of demographic stability for each metapopulation in our analysis - Constancy and Persistence Stability (Grimm and Wissel 1997). Constancy, as the name indicates, refers to how unchanging or constant the size of a population is. In other words, the less the size of a population fluctuates, the more stable it is in terms of constancy. We measured constancy stability using Fluctuation Index (henceforth, FI; Dey and Joshi 2006), which is formulated as $\sum|N_{t+1}-N_t| / (\bar{N}\times T)$, where N_t is the population size after perturbation (if applicable) at time t, $\bar{N}$ is the average population size over T generations. Thus, the lower the FI is, the higher is the constancy stability.

In contrast, persistence can be said to be the resistance of a population to extinction or the converse of the propensity of a population to go extinct, which is quantified by computing extinction probability (henceforth, EP) = E/T, where E is the number of extinction events in T number of generations.

Additionally, we measured genetic stability of the metapopulations by computing their effective population size (EPS). This is computed as the harmonic mean (Allendorf et al. 2012) of post-perturbation (if applicable) population size, *i.e.* mathematically, EPS = $T/\sum(1/N_t)$, where T is the length of the timeseries and N_t is breeding population size at the t^{th} generation.

Synchrony between the subpopulations of a metapopulation is quantified by computing the cross-correlation coefficient at lag zero of the first-differenced time series of log-transformed values of the two subpopulation sizes (Bjørnstad et al. 1999; Dey and Joshi 2006).

2.5. Population stability methods

For this comparative analysis, we considered six population stability methods - Constant Pinning (CP, McCallum 1992b; Parthasarathy and Sinha 1995; Solé et al. 1999), Lower Limit Control (LLC, Hilker and Westerhoff 2005), Adaptive Limiter control (ALC, Sah et al. 2013a), Upper Limit Control (ULC, Hilker and Westerhoff 2005), Target Oriented Control (TOC, Dattani et al. 2011), and Both Limit Control (BLC, Tung et al. 2014). These methods were chosen because they are implementable in real biological settings (Gusset et al. 2009), well studied theoretically (McCallum 1992b; Solé et al. 1999; Hilker and Westerhoff 2005; Dattani et al. 2011; Tung et al. 2014), and been validated empirically (Dey and Joshi 2007, 2013; Sah et al. 2013a; Tung et al. 2016a,b). Additionally, efficiency of these six methods had recently been compared in spatially-unstructured populations (Tung et al. 2014), which can be contrasted qualitatively with the results we obtain in the context of spatially-structured populations in this study. Outcomes of these two studies together will provide us a wholistic picture of stabilizing extinction-prone populations. Mathematical formulation of the six methods and corresponding control parameter values are presented in Table S1. A more detailed description of these methods can be found elsewhere (Tung et al. 2014).

2.6.The comparative framework

After implementing the methods on our spatially-structured simulation framework, we first tested the performance of the methods by measuring two aspects of population stability – constancy and persistence, over a range of control parameters (ranges can be found in Table 2). Promisingly, similar to the analysis of spatially-unstructured populations, we also have observed that any level of constancy and persistence stability can be achieved in case of two-patch metapopulations by varying the control parameters of all six methods. However, in order to reach a specific level of stability in one aspect of stability the methods varied substantially in their performance for the other aspect of stability and/or costs incurred in terms of external perturbation needed to reach this level of stability.

So, in order to compare the effectiveness of these methods at a common level, we decided to look at the performance of the methods in order to achieve 50% reduction of fluctuation index (*i.e.*, improvement of constancy stability) and 50% reduction of extinction probability (*i.e.*, improvement of persistence stability), separately. For each of these two scenarios, we compared the methods using an established composite performance score (Tung et al. 2014) and a novel robustness index of the performance of the methods against noise in census count.

2.7.Composite Performance Score

Composite performance score (CPS) or composite index (following Tung et al. 2014), gives equal weightage to the effort magnitude and effective population size and the other stability value (*i.e.*, extinction probability when analysing for 50% reduction of fluctuation index, and vice versa). Here, effort magnitude (EM) can be translated as the ‘cost’ of applying a certain control method to the metapopulation and computed as $\square\ |a_t-b_t| / (N\square \times T)$, where, b_t and a_t denote population size before and after applying the control method, and $N\square$ denotes the average population size over T generations.

The scales of the components of CPS, or “component indices” (CI), are different. This would bias our comparison by giving more weightage to CIs with values a higher scale. To alleviate this bias, the value for each of the CIs for each method was divided by the highest of that index amongst all methods. This way, the scaled value of all the CIs remained between 0 to 1. It is also noted that although a lower value of $CI_{FI/EP}$ (component index for FI or EP) and CI_{EM} (component index for EM) are desirable for better performance of a method, for CI_{EPS} (component index of effective population size), a *higher value* will denote better performance. Thus, we computed composite performance index as, $CI_{FI/EP} + CI_{EM} + (1-$

CI_{EPS}), and overall, the lower the composite score for a method is, the better it works in stabilising the regime in question.

For Lr populations, we found that the metapopulations were extremely persistent stable, i.e., they had negligibly low EP even without any external perturbations (refer to Section 3.1). Therefore, we felt that including CI_{EP} in the calculations for composite performance score for 50% reduction in FI in Lr regimes would unnecessarily bias the results by reflecting a method's ability of solving a problem (i.e., extinction) that was not there. Therefore, we decided to not include CI_{EP} in the calculation of composite performance score for reducing FI by 50% in Lr regimes.

2.8. Robustness Analysis

A notable challenge with external perturbation-based control methods is the need for precise census counts in each generation when introducing or removing individuals, with the exception of the constant pinning method. In natural settings, obtaining an exact animal count is nearly impossible. Typically, only an estimate of the census size is achieved, which can lead to overestimations or underestimations of the actual population size per generation. The impact of such census errors on the efficacy of control methods remains unexplored. To address this, we conducted a CPS-based comparison incorporating varying levels of white noise in census values. This allowed us to simulate random overestimations or underestimations in each generation. We varied the noise level from 0 to 50% in increments of 5%. Hence, the perceived population size used for implementing control methods was defined as: *actual population size* ± *(noise level* × *actual population size)*. Control methods were applied based on this potentially erroneous population size. Subsequently, we calculated the "robustness index" to evaluate the impact of the error. This index was computed as the *mean of (composite_score_with_error – composite_score_without_error)^2* for each noise level, serving as a measure of dispersion around the no-error composite performance score. In addition, factors like weather conditions, landscape characteristics, and vegetation density can influence the accuracy of population estimates with specific biases. To capture this, we considered two types of errors: positive noise (overestimating population) and negative noise (underestimating population). For each error type, rates ranged from 0 to 0.5 in increments of 0.05, enabling us to track the composite index's trajectory against error rates. Although component indices were derived from the averages of 70 replicates, minor differences in composite scores emerged in repeated runs of the same code. To address this, we computed the composite scores 20 times, using the average of these scores to represent the composite index in our graphical representation. The results for these can be found in Supplementary Figures S8 - S13.

3. Results and Discussion

3.1 Dynamics of the unperturbed regimes

Initially, we evaluated the dynamics of unperturbed metapopulation regimes – those not subjected to any population stability methods – to establish a baseline for subsequently comparing the efficacy of various population stability strategies. For this purpose, we estimated two aspects of demographic stability – constancy and persistence – as well as genetic stability by computing effective population size for all 12 regimes (Figure 1). This analysis reveals how these stability aspects are influenced by the complex interplay of intrinsic growth rate, carrying capacity of the constituent subpopulations, and migration rate between the subpopulations. Additionally, this analysis serves as a vital reference point for understanding the efficacy of population stability methods in these specific metapopulation regimes.

Population size fluctuation index and extinction probability values as a measure of inverse of constancy and persistence stability respectively of the unperturbed dynamics clearly suggested that the regimes with high intrinsic growth rate and low carrying capacity (i.e. HrLk regimes) exhibited the most unstable metapopulation dynamics (Figure 1a-1d). The instability in these dynamics stems from overcrowding due to high intrinsic growth rates, further aggravated by limited resource availability due to the low carrying capacities of these regimes. This led to overutilization of resources, resulting in characteristic ‘boom-bust dynamics’ with significant population fluctuations and a heightened risk of extinction (Grimm and Wissel 2004; Tung et al. 2014; Figure S1). These regimes experienced severe population bottlenecks nearly every alternate generation, resulting in relatively poor genetic stability, as indicated by low effective population sizes (Figure 1e-1f). Interestingly, this study also showed that this pattern remained consistent regardless of the high or low level of migration and whether the nature of migration between the subpopulations is symmetric or asymmetric (comparing Figure 1a and Figure 1b; comparing Figure 1c and Figure 1d).

Regimes characterized by high intrinsic growth rates and high carrying capacities, termed HrHk regimes, emerged as the subsequent most unstable scenarios, as indicated by their high fluctuation indexes, implying low constancy stability (Figure 1a, 1b). Notably, though these regimes exhibited 'boom-bust dynamics' (Figure S1), their high carrying capacities resulted in a significantly reduced frequency of population size reaching zero, as evidenced by their relatively low extinction probabilities (Figure 1a, 1b; also see Tung et al. 2014). Despite reaching higher population sizes due to their ample carrying capacities, these regimes did not necessarily see an increase in effective population size (Figure 1e, 1f). This is attributed to the substantial fluctuations in population size and that the calculation of effective population size is more adversely impacted by smaller population values (Allendorf et al. 2012).

An intriguing characteristic of HrHk regimes, especially those with symmetric migration, is the observed difference in metapopulation constancy stability between low and high migration levels (Figure 1a). Metapopulation with low migration level exhibited substantially lower fluctuation index i.e. greater constancy stability than those with high migration, although constancy of the constituent subpopulations was comparable. This apparent discrepancy is resolved when we look into the level of synchrony between the constituent subpopulations and found that synchrony level was much lower in metapopulations with low migration level i.e. in case of HrHkLm regime compared to metapopulations with high migration level i.e. in case of HrHkHm regime. This result captured previously reported out-of-phase dynamics of coupled unstable populations seen both theoretically (Gyllenberg et al. 1993b; Doebeli 1995; Amarasekare 1998; Kendall and Fox 1998; Ylikarjula et al. 2000; Briggs and Hoopes 2004; Dey and Joshi 2006; Abbott 2011; Dey et al. 2014) and empirically (Lecomte et al. 2004; Dey and Joshi 2006; Sah et al. 2013b; Mueller and Joshi 2020).

Similarly, in metapopulations with low intrinsic growth rates, we observed enhanced constancy stability, which correlates with a lower synchrony level between subpopulation dynamics, especially in scenarios of low symmetric migration (as seen in the comparison of fluctuation index and synchrony plots for LrLkLm vs LrLkHm, and LrHkLm vs LrHkHm, Figure 1a, 1g). Comparing both constancy and persistence stability, metapopulations with low intrinsic growth rate (Lr regimes) were found to be more stable demographically compared to the regimes with high intrinsic growth rate i.e. Hr regimes. The contrast is more prominent in terms of persistent stability, as irrespective of the level and nature of migration, metapopulations with Lr regimes rarely incurred extinction (Figure 1c-1d). However, it is noteworthy that despite enhanced demographic stability, genetic stability of LrLk regimes is not high. This is primarily because these regimes tend to maintain low population sizes due to their lower carrying capacities and growth rates, making them more vulnerable to inbreeding depression and loss of genetic diversity.

In stark contrast, LrHk regimes exhibited more stable dynamics with significantly higher average population sizes, leading to considerably larger effective population sizes (Figure 1e-1f). This divergence highlights the complex relationship between demographic and genetic stability in metapopulations, influenced by intrinsic growth rates and carrying capacities.

Additionally, our study showed that the stability properties of metapopulations with asymmetric migration lie between those of the two symmetric cases (Figure 1). This result is in contrast to the notion that metapopulations with asymmetric migration rate are more stable (Doebeli 1995; Ylikarjula et al. 2000). Instead, it aligns with more recent research suggesting that the relative stability of metapopulations with asymmetric migration is contingent on specific contextual factors (Dey et al. 2014).

Taken together, the 12 regimes considered in this study, each with their unique combinations of demographic and genetic stability attributes, provide a robust framework for analyzing the effectiveness of population stability methods across a range of scenarios. This comprehensive approach allows us to synthesize the results within a consistent comparative framework, thereby facilitating the derivation of broader conclusions about population stability strategies in diverse ecological contexts.

3.2 Comparing the control methods for inducing desired constancy stability

To assess the relative performance of the control methods on a common platform, we first computed composite performance score (following Tung et al. 2014) for each of the methods in each regime separately. This score integrated other stability measures, such as extinction probability and effective population size, along with a metric for implementation effort, in order to diminish population size fluctuation to 50% of the unperturbed scenario, thereby improving constancy stability. As the extinction probabilities for Lr populations were found to be negligible (Figure 1c-1d), we excluded the extinction probability component from the calculation of composite scores in Lr regimes. This approach was adopted based on previous findings that, while all methods can independently promote various stability aspects, they often entail trade-offs in terms of other stability facets or require significant implementation efforts (Tung et al. 2014, 2016a,b). For a comprehensive assessment, we calculated these composite scores for each method across all 12 regimes. In this scoring system, a lower composite score indicates a more favourable performance, reflecting a method's efficacy in enhancing stability with minimal trade-offs and effort.

Our findings indicate that the effectiveness of control methods in metapopulations is context-dependent, with no single method proving universally optimal across all regimes. This aligns with previous observations in spatially unstructured populations (Tung et al. 2014). However interestingly, our comparative analysis revealed a common trend for the regimes with low intrinsic growth rate (i.e. Lr regimes). In these regimes, lower limiter control (LLC), adaptive limiter control (ALC) and both limiter control (BLC) demonstrated similar composite scores and consistently outperformed other methods. These are closely followed by target-oriented control (TOC) and upper limiter control (ULC), in the order of performance. Constant pinning (CP) method performed consistently worst in all six scenarios. The reason behind this trend became clear when we checked the individual components – effective population size and effort magnitude that constituted the composite score in these scenarios (Figure S2-S4). LLC, ALC, and BLC achieved effective population sizes that were comparable and only lower than those induced by the CP method. Although CP had the potential to maximize effective population size across the regimes, its high implementation costs, as evidenced by substantial effort magnitude, made it the least favourable option. In contrast, LLC, ALC, and BLC struck a balance, attaining moderate effective population sizes with reasonable level of implementation efforts to become the best performing methods in these regimes.

In HrLk regimes, LLC stood out as the superior method compared to others. It paralleled ALC in enhancing effective population size. However, LLC surpassed ALC in reducing implementation effort and extinction probability, establishing itself as the most effective method in these scenarios. While ULC and BLC proved more efficient in mitigating extinction risks, their higher implementation costs and lower effective population sizes negatively impacted their overall rankings according to the composite scores. On the other hand, in HrHk regimes, BLC demonstrated superior efficacy, successfully eliminating extinction risks while achieving an optimal balance between effort and effective population size.

3.3 Comparing the control methods for inducing desired persistence stability

In our subsequent analysis, we focused on the performance of control methods in reducing the extinction probability to 50% of the corresponding unperturbed scenario. Since Lr regimes infrequently experience extinction, this analysis was restricted to Hr regimes. Here, the composite performance score was derived from the fluctuation index, effective population size, and the magnitude of implementation effort (following Tung et al. 2014).

We found that ALC was the most effective method across all Hr regimes (see Figure 3), closely followed by LLC, BLC, and CP. In contrast, ULC and TOC were less effective in addressing extinction risk. It appears that methods designed to prevent population size from dropping below a certain threshold – whether constant (as in CP, LLC and BLC) or variable (as in ALC) – are more successful in enhancing a population's resistance to extinction. In contrast, the methods that involve culling individuals to counter overpopulation, i.e., TOC and ULC, do not seem to make the metapopulation more persistent.

Interestingly, although we found that ALC performed the best in terms of inducing desired persistence stability in all the regimes, analysis of the components of composite score revealed that it becomes the best through distinct routes (Figure S5-S7). In case of the most unstable HrLk regimes, when migration rate between the subpopulations was low (i.e. for HrLkLm regime), CP induces the maximum effective population size followed by LLC, ALC and BLC. But CP did that at the cost of a large effort magnitude leading to its poor performance rank based on composite score. Among LLC, ALC and BLC, ALC performed the best with respect to curbing population size fluctuation at the cost of minimum effort magnitude, leading it to the best metapopulation stability method in this regime. In scenarios with high migration rate between the subpopulations i.e. in HrLkHm regime, effort magnitude for LLC was minimum but this led to very low effective population size and thereby compromising its performance score. Other trends were similar, and overall ALC become the best performing method. While migration between the subpopulations was asymmetric i.e. in HrLkLmHm regime, effort magnitude incurred by ALC to reach the desired level of persistence stability was actually the maximum, but as this method was excellent in simultaneously improving constancy stability and genetic stability, it became the best performing method with lowest overall composite score. While carrying capacity was high, ALC reduced population size fluctuation and increased effective population size to the maximum extent with moderate effort magnitude. While LLC and BLC also performed well, they fell short in terms of one or more components of the composite performance score.

To offer a comprehensive overview of the efficacy of six population stability methods in achieving target levels of constancy and persistence stability, we have compiled a summary table that aggregates the rankings for each method across all evaluated regimes (Table S3). Our consolidated findings indicate that the Lower Limiter Control (LLC) method delivers consistent results in attaining the desired level of constancy stability, while the Adaptive Limiter Control (ALC) method stands out as the most effective for achieving the desired level of persistence stability. These results provide actionable insights for population ecologists and conservation biology practitioners, without going into the details of the specific regime conditions, aiding in the formulation of intervention strategies in case of spatially-structured populations.

3.4 Comparing robustness of the control methods against census noise

To evaluate the robustness of stability methods against variations in census accuracy, we compared the composite performance scores of these methods across a spectrum of white noise levels in population census counts. This approach addresses a significant concern in implementing external perturbation methods: the need for precise census counts of the target species, which may not always be readily available. We specifically analysed the impact of census noise on achieving the above-mentioned desired levels of constancy and persistence stability.

In scenarios focused on enhancing constancy stability, particularly within low intrinsic growth rate regimes (i.e., Lr regimes), the performance of most methods was comparable and robust, with the exception of ULC (Figure 4; Supplementary Figure S8). Combining their overall performance with resistance to census noise, LLC, ALC, and BLC emerged as the most promising methods in these regimes. Whereas, in HrLk regimes, LLC, ALC, and TOC demonstrated greater robustness to census noise. Consequently, LLC stood out as the most promising method in these settings. For HrHk regimes, LLC, TOC, BLC when migration rate is low between the subpopulations, ALC, TOC when migration rate is high between the subpopulations and LLC, ALC, TOC and BLC when migration rate is asymmetric between the subpopulations performed the better against census noise. Thus, combining performance of the methods and their robustness against census noise, BLC stood out to be promising in these regimes, although one needs to note that it is less robust to census noise when migration rate is high between the subpopulations.

When focusing on inducing persistence stability to a desired level, ULC performed poorly for HrLk regimes. Other methods performed similarly. In case of asymmetric migration between the subpopulations ALC performed the best, closely followed by TOC (Figure 5;

Supplementary Figure S9). Whereas, all methods performed well in HrHk regimes, ALC being good consistently. Thus, considering both performance and robustness to census noise, ALC was identified as the most effective method in these regimes.

In order to present a comprehensive evaluation of the resilience of the six control methods to census inaccuracy in presence of white noise, we aggregated the rank of robustness indices of these methods for inducing both constancy and persistence stability into a summarizing table (Table S4). This analysis offers a broad view of each method's resilience to noise-induced variability, independent of specific ecological regime parameters. When focusing on attaining a target level of constancy stability, our results indicate a notable parity in performance among all methods except for the Upper Limiter Control (ULC), which exhibited subpar robustness. Conversely, in the pursuit of persistence stability, the Target-Oriented Control (TOC), Adaptive Limiter Control (ALC), Lower Limiter Control (LLC), and Constant Pinning (CP) methods demonstrated marginally superior resilience, in descending order of effectiveness.

Performance of ALC was found to be rather resilient in the presence of a range of intensities of positive (i.e. overestimation; Supplementary Figure S10-S11) and negative (i.e. underestimation; Supplementary Figure S12-S13) noise to census. Composite score of ULC methods was found to be the most variable across ranges of noise intensities. Notably, the CP method, which is theoretically independent of population census data, was expected to excel irrespective of census noise levels. However, contrary to expectations, CP did not surpass other methods in terms of composite score performance even in the presence of census noise.

Conclusion

In conclusion, our comprehensive analysis of six methods for stabilizing metapopulation dynamics, along with their robustness against census noise, reveals significant insights into the complex interplay of demographic, genetic, and migration-related factors in population stability. In comparing control methods, no single approach emerged as universally superior across all regimes. However, in order to induce constancy stability to a desired level, lower limiter control (LLC), adaptive limiter control (ALC), and both limiter control (BLC) proved most effective in Lr regimes. LLC excelled in HrLk regimes by balancing efficacy and effort, and BLC was the method of choice in HrHk regimes for its ability to eliminate extinction risks effectively. Remarkably, ALC stood out for inducing persistence stability across all regimes, achieving the best performance through distinct pathways in different migration scenarios. Our findings underscored the importance of considering the specific aspects of stability when selecting and implementing stabilization methods. Furthermore, our analysis of robustness against census noise highlights the practicality of these methods in real-world scenarios, with LLC, ALC, and BLC showing promising results in various regimes. This study not only contributes to our understanding of metapopulation dynamics but also offers practical guidance for selecting appropriate stability methods in varied ecological contexts. It highlights the need for a nuanced, context-specific approach when implementing population stability strategies for effective ecological management and conservation efforts.

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Figure Legends

Figure 1. Unperturbed Metapopulation Dynamics. This figure presents various indices of population dynamics across 12 distinct regimes. Indices for subpopulations and the overall metapopulation are displayed separately, with the left set of graphs (a, c, e, g) illustrating symmetric migration scenarios and the right set (b, d, f, h) depicting asymmetric migration. The indices detailed include: Fluctuation Index (FI) in (a) and (b), highlighting dynamic variability; Extinction Probability (EP) in (c) and (d), with Lr regimes displaying negligible to zero EP; Effective Population Size (EPS) in (e) and (f), representing genetic diversity; and Synchrony between subpopulations in (g) and (h). Standard error was used as error bars. For some cases, error bars are too small to be visible.

Figure 2. Composite Performance Scores for 50% Reduction in Fluctuation Index. Presented here are the composite performance scores for six population control methods evaluated across 12 distinct regimes, with the objective of achieving a 50% decrease in Fluctuation Index to promote constancy stability. Atop each bar, the numerical annotations represent the performance ranking of the method, with a lower composite score denoting a superior rank. Standard error is depicted as the error bars; however, in certain instances, the error bars are too small to be visible.

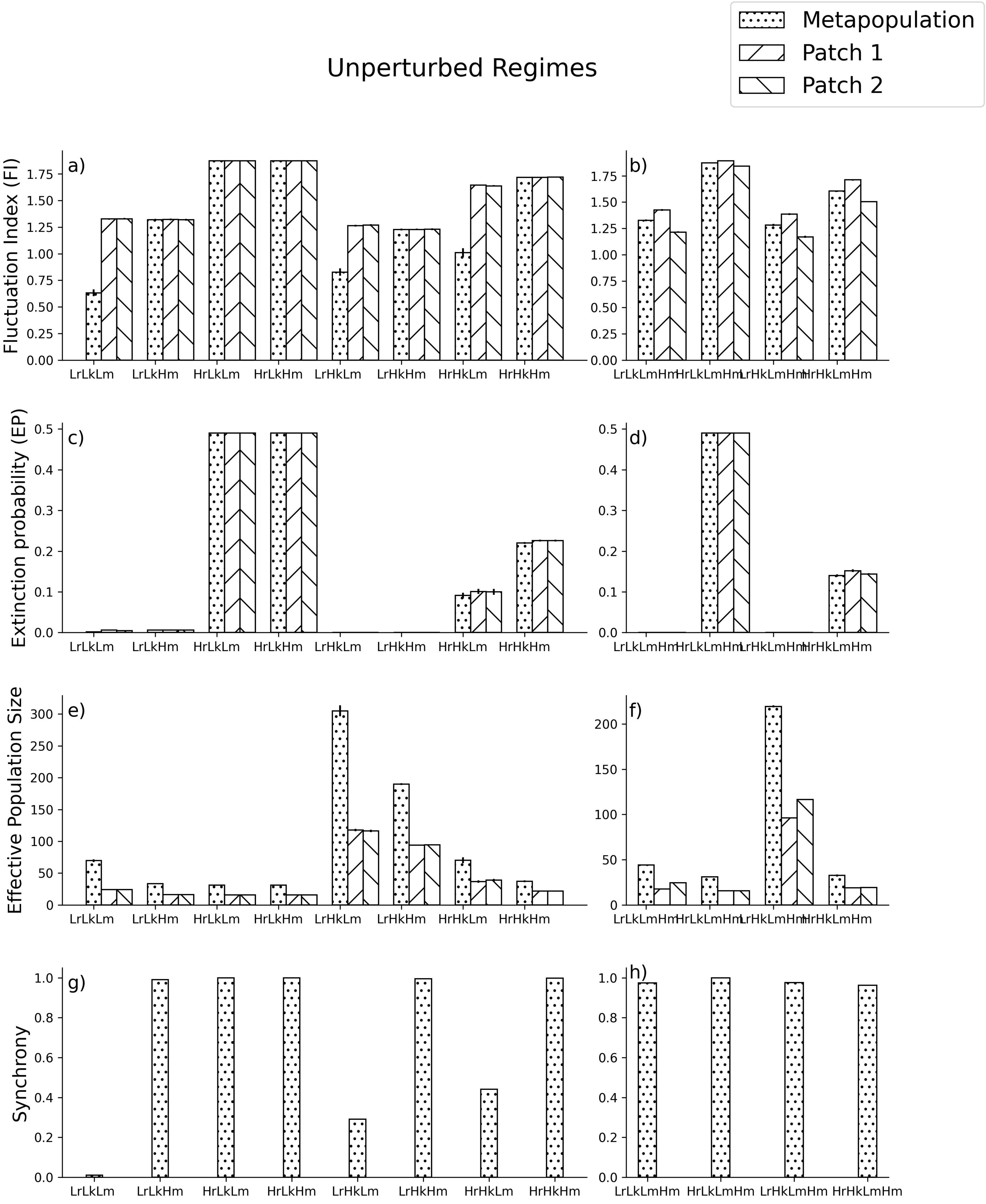
Figure 3. Composite Performance Scores for 50% Reduction in Extinction Probability. Presented here are the composite performance scores for six population control methods evaluated across six regimes, with high intrinsic growth rate (i.e. Hr regimes) while achieving a 50% decrease in Extinction Probability to promote persistence stability. Atop each bar, the numerical annotations represent the performance ranking of the method, with a lower

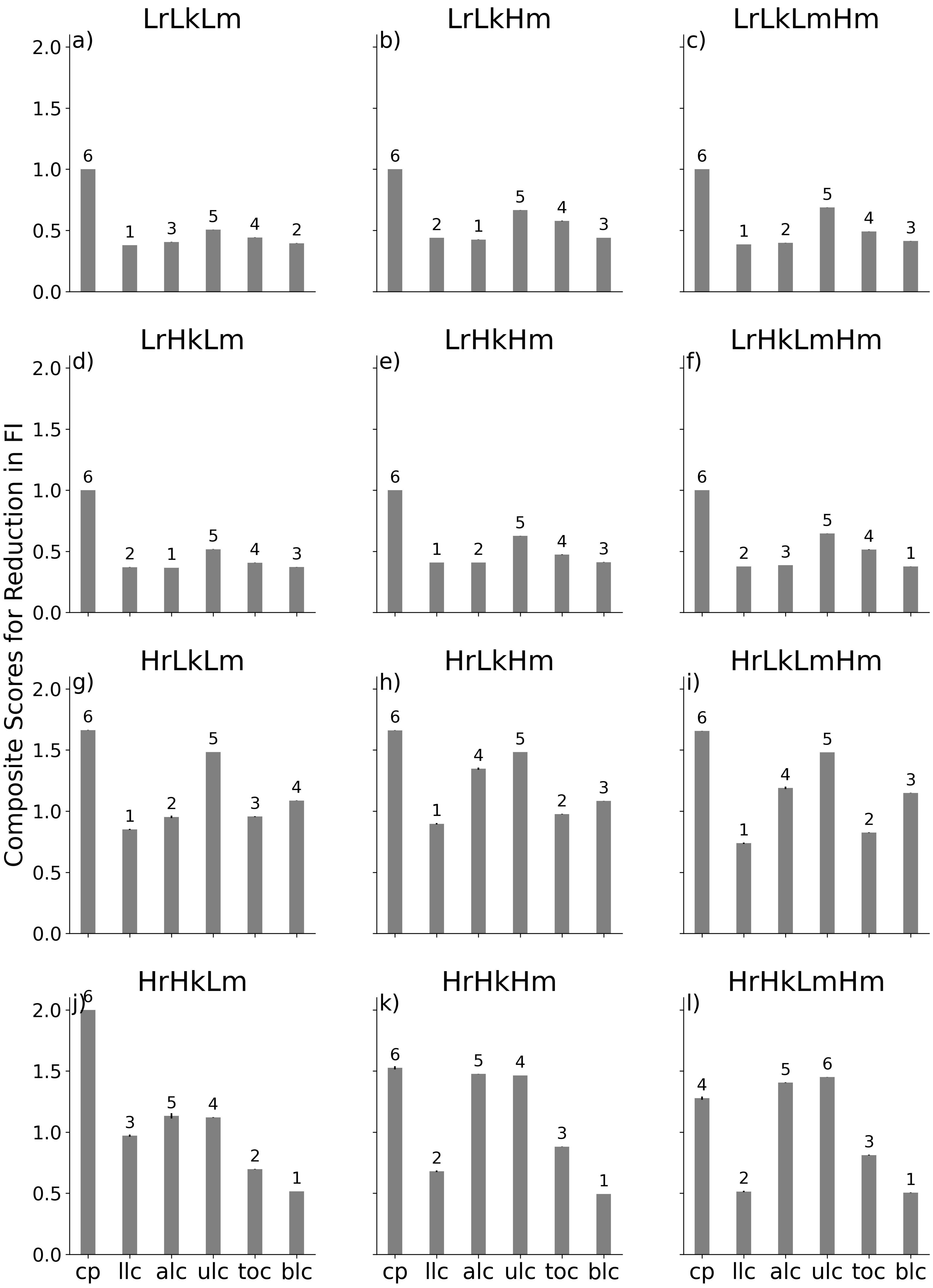
composite score denoting a superior rank. Standard error is depicted as the error bars; however, in certain instances, the error bars are too small to be visible.

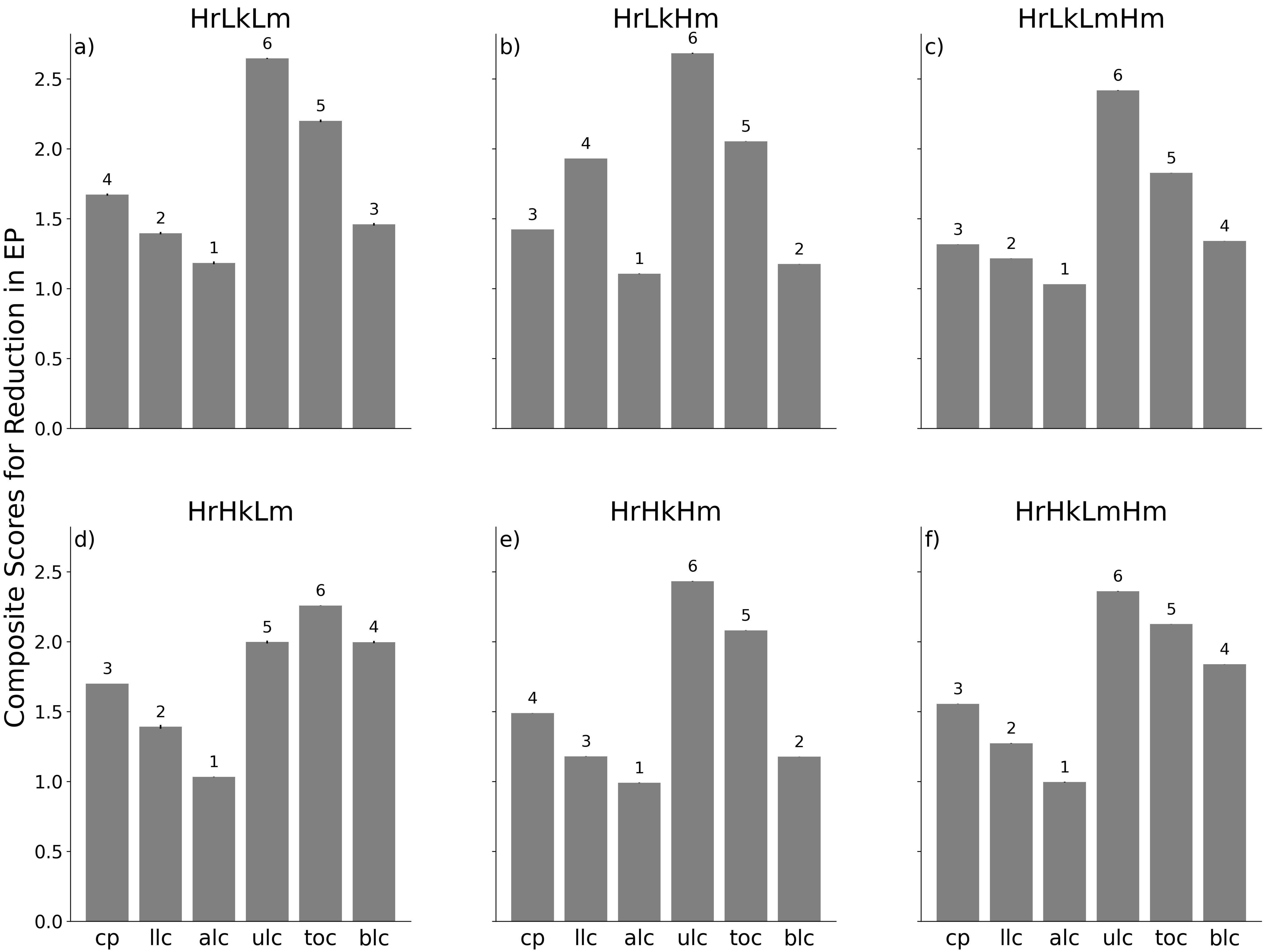
Figure 4. Robustness Indices for Population Stability Methods While Inducing Constancy Stability Under Varying White Noise Levels. This figure displays the robustness indices of six population stability methods evaluated across 12 distinct regimes tasked with inducing constancy stability, specifically a 50% reduction in the Fluctuation Index, in the presence of different intensities of white noise affecting population size estimates. The robustness index is determined by the average squared deviation between composite scores obtained under various white noise levels and that derived in the absence of noise. This metric evaluates the consistency of each method's performance in the face of census accuracy. To present the complete data range within one frame, a discontinuous Y-axis has been employed. Numerical annotations above each bar indicate the method's robustness rank, with lower scores corresponding to higher robustness against noise. Standard errors are represented by error bars. In certain instances, the error bars are too small to be visible.

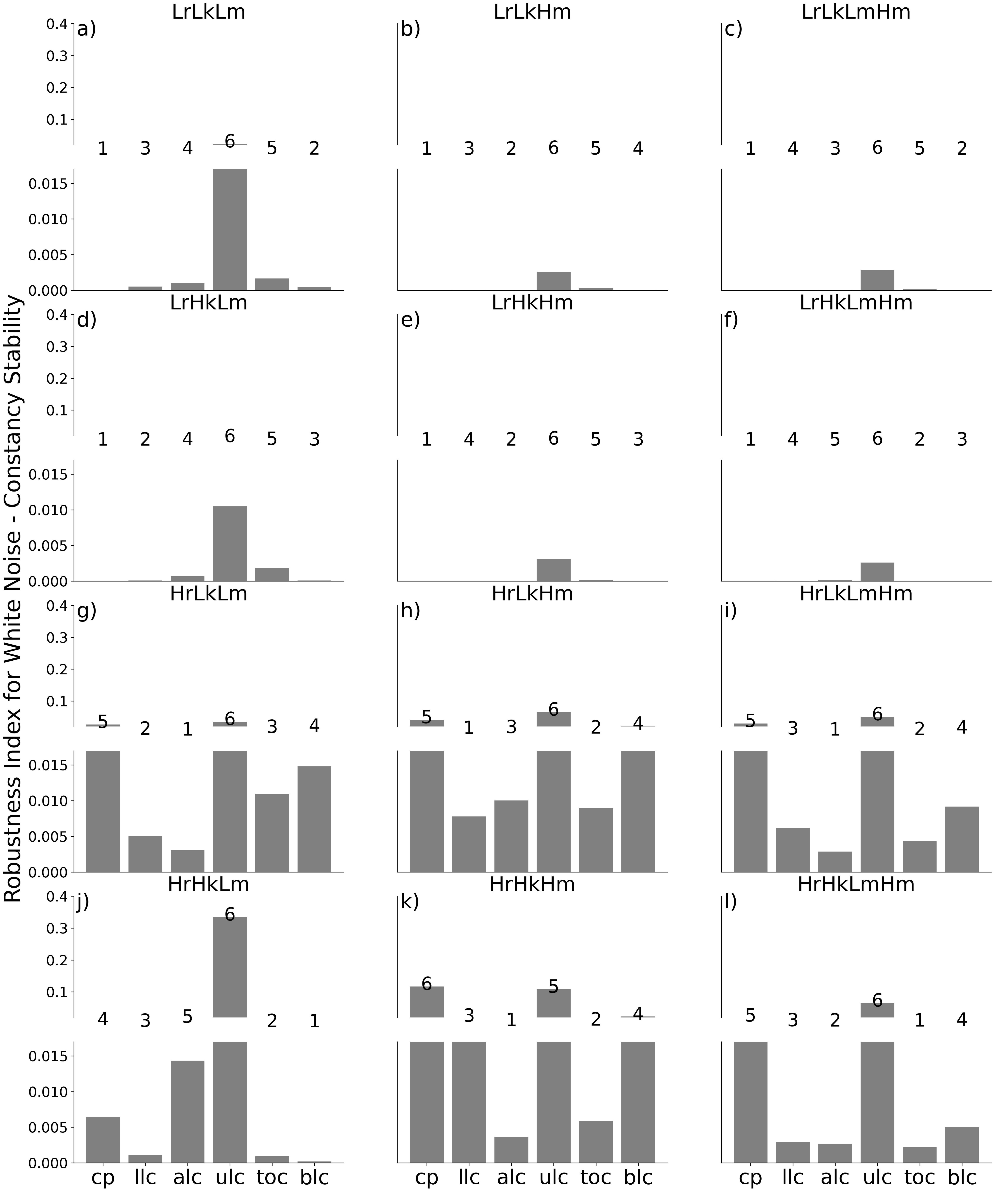
Figure 4. Robustness Indices for Population Stability Methods While Inducing Persistence Stability Under Varying White Noise Levels. This figure displays the robustness indices of six population stability methods evaluated across six regimes with high intrinsic growth rate i.e. Hr regimes aimed to induce persistence stability, specifically a 50% reduction in the Extinction Probability, in the presence of different intensities of white noise affecting population size estimates. The robustness index is determined by the average squared deviation between composite scores obtained under various white noise levels and

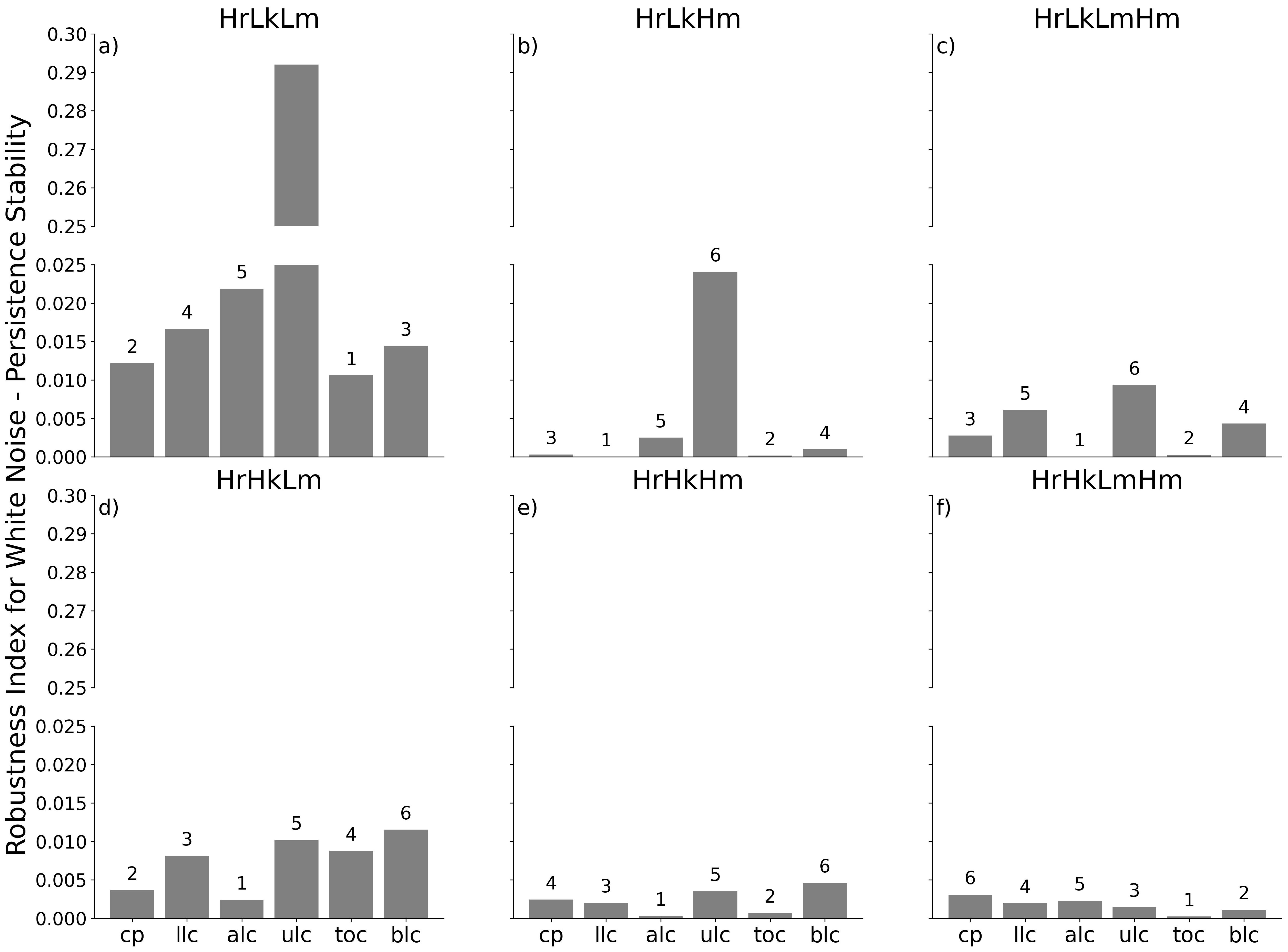
that derived in the absence of noise. This metric evaluates the consistency of each method's performance in the face of census accuracy. To present the complete data range within one frame, a discontinuous Y-axis has been employed. Numerical annotations above each bar indicate the method's robustness rank, with lower scores corresponding to higher robustness against noise. Standard errors are represented by error bars. In certain instances, the error bars are too small to be visible.


Unperturbed Regimes
Metapopulation
Patch 1
Patch 2
a)
b)
c)
d)
e)
f)
g)
h)
Fluctuation Index (FI)
Extinction probability (EP)
Effective Population Size
Synchrony
0.00
0.25
0.50
0.75
1.00
1.25
1.50
1.75
0.0
0.1
0.2
0.3
0.4
0.5
0
50
100
150
200
250
300
0.0
0.2
0.4
0.6
0.8
1.0
LrLkLm
LrLkHm
HrLkLm
HrLkHm
LrHkLm
LrHkHm
HrHkLm
HrHkHm
LrLkLmHm
HrLkLmHm
LrHkLmHm
HrHkLmHm


Composite Scores for Reduction in FI
LrLkLm
a)
6 1 3 5 4 2
LrLkHm
b)
6 2 1 5 4 3
LrLkLmHm
c)
6 1 2 5 4 3
LrHkLm
d)
6 2 1 5 4 3
LrHkHm
e)
6 1 2 5 4 3
LrHkLmHm
f)
6 2 3 5 4 1
HrLkLm
g)
6 1 2 5 3 4
HrLkHm
h)
6 1 4 5 2 3
HrLkLmHm
i)
6 1 4 5 2 3
HrHkLm
j)
6 3 5 4 2 1
HrHkHm
k)
6 2 5 4 3 1
HrHkLmHm
l)
4 2 5 6 3 1
0.0
0.5
1.0
1.5
2.0
cp
llc
alc
ulc
toc
blc


HrLkLm
a)
HrLkHm
b)
HrLkLmHm
c)
HrHkLm
d)
HrHkHm
e)
HrHkLmHm
f)
Composite Scores for Reduction in EP
0.0
0.5
1.0
1.5
2.0
2.5
cp
llc
alc
ulc
toc
blc
a) 4 2 1 6 5 3
b) 3 4 1 6 5 2
c) 3 2 1 6 5 4
d) 3 2 1 5 6 4
e) 4 3 1 6 5 2
f) 3 2 1 6 5 4


Robustness Index for White Noise - Constancy Stability
a) LrLkLm
b) LrLkHm
c) LrLkLmHm
d) LrHkLm
e) LrHkHm
f) LrHkLmHm
g) HrLkLm
h) HrLkHm
i) HrLkLmHm
j) HrHkLm
k) HrHkHm
l) HrHkLmHm
0.4
0.3
0.2
0.1
0.015
0.010
0.005
0.000
a) 1 3 4 6 5 2
b) 1 3 2 6 5 4
c) 1 4 3 6 5 2
d) 1 2 4 6 5 3
e) 1 4 2 6 5 3
f) 1 4 5 6 2 3
g) 5 2 1 6 3 4
h) 5 1 3 6 2 4
i) 5 3 1 6 2 4
j) 4 3 5 6 2 1
k) 6 3 1 5 2 4
l) 5 3 2 6 1 4
cp
llc
alc
ulc
toc
blc


Robustness Index for White Noise - Persistence Stability
HrLkLm
a)
HrLkHm
b)
HrLkLmHm
c)
HrHkLm
d)
HrHkHm
e)
HrHkLmHm
f)
0.30
0.29
0.28
0.27
0.26
0.25
0.025
0.020
0.015
0.010
0.005
0.000
a) 2 4 5 1 3
b) 3 1 5 6 2 4
c) 3 5 1 6 2 4
d) 2 3 1 5 4 6
e) 4 3 1 5 2 6
f) 6 4 5 3 1 2
cp
llc
alc
ulc
toc
blc