Entomology

# Species richness and survival constraints of predatory ladybird beetles (Coleoptera: Coccinellidae): A review of abiotic and biotic mortality factors

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**Abstract**

**Objectives:** To synthesize evidence on species richness of predatory ladybird beetles and the stage-specific abiotic, biotic and management-related factors that constrain their survival, recruitment and persistence in agroecosystems.

**Methods:** A critical narrative review was developed from foundational and recent literature on Coccinellidae richness, temperature and moisture effects, prey-dependent performance, cannibalism, intraguild predation, predators, parasitoids, pathogens and pesticide effects. Quantitative claims were retained when attributable to specific studies.

**Results:** Ladybird richness represents a regional species pool rather than guaranteed biological-control capacity. Temperature, moisture and rainfall can alter development, survival, activity and disease risk. Prey limitation can reduce growth and reproduction and intensify cannibalism and intraguild predation. Parasitoids, pathogens, external predators and pesticide exposure further reduce recruitment. Recent life-table evidence identifies the first larval instar as a major mortality bottleneck in several aphidophagous species.

**Conclusions:** Realized biological-control function depends on sequential survival from egg to reproductive adult, not on richness alone. Field life tables, multifactor experiments and region-specific demographic studies are needed to quantify interacting mortality processes and improve conservation and deployment of predatory Coccinellidae.

**Keywords:** Biological control, Coccinellidae, Cannibalism, Intraguild predation, Life table, Parasitoids

## 1. Introduction

Ladybird beetles (Coleoptera: Coccinellidae) are among the most conspicuous predatory insects in agricultural ecosystems. Aphidophagous and other predatory coccinellids consume aphids, scale insects, mealybugs, whiteflies, mites and other small arthropods and have long been incorporated into classical, augmentative and conservation biological-control programmes [1-3]. Their value, however, depends not simply on the presence of species in a crop but on whether sufficient numbers survive, reproduce and remain in the habitat long enough to exert predation pressure.

Coccinellidae is a species-rich family. Contemporary reviews commonly refer to approximately 6,000 described species worldwide, although the number is necessarily dynamic as taxonomic revisions and new species descriptions continue 4. For the Indian subregion, Poorani [5] documented 400 species, including six subspecies, in 79 genera while excluding Epilachninae. More recent taxonomic work continues to add records and species; for example, Poorani et al. [6] revised Indian Plotinini from six species in three genera to nine species in four genera and described a new species from the Western Ghats. Thus, richness is not a fixed inventory and should not be equated with the number of species that are abundant or functionally important in a particular crop.

Field assemblages illustrate this distinction. In San Cristóbal Island, Galápagos, Peñaherrera-Romero et al. [7] catalogued 19 coccinellid species across natural and human-modified habitats, but endemic taxa were scarce and habitat-restricted whereas Cycloneda sanguinea was broadly prevalent and the non-native Cheilomenes sexmaculata was associated mainly with disturbed habitats. Such patterns emphasize that taxonomic richness, local dominance and ecological persistence are different properties of a community.

Mortality provides the demographic link between these properties. Eggs, successive larval instars, pupae and adults differ in mobility, physiology, resource requirements and exposure to natural enemies. Consequently, the same environmental event or biological interaction may have very different consequences depending on developmental stage. Recent life-table evidence reinforces this point: Agarwala [8] found the first larval instar to be the stage of greatest mortality in three aphidophagous ladybird species, although the magnitude and causes differed among a specialist and two generalists.

Previous reviews have synthesized ladybird ecology, predator–prey dynamics, behaviour, habitat management and symbiotic relationships [2-4]. The present review adopts a complementary demographic perspective. It integrates abiotic stress, resource limitation, cannibalism, intraguild predation, external predation, parasitoids, pathogens and agricultural management across the life cycle, with emphasis on how these filters determine recruitment to the adult population and therefore population persistence and realized biological-control function. The central proposition is that species richness describes which taxa are present, whereas stage-specific survival determines which taxa persist and contribute substantially to pest suppression.

**Review approach and scope**

This is a critical narrative review rather than a formal systematic review or meta-analysis. The evidence base was assembled from the seminar literature set and expanded through targeted searches of recent and foundational literature on Coccinellidae richness, life-history responses to temperature, prey-dependent functional responses, cannibalism, intraguild predation, parasitoids, pathogens and pesticide effects. Priority was given to primary experimental or field studies for quantitative claims, taxonomic revisions for richness estimates, and major monographs or reviews for established ecological concepts. Numerical values are reported only when attributable to a specific study or synthesis; broad seminar-style ranges without traceable primary support were not retained. The review focuses on predatory Coccinellidae, especially aphidophagous species relevant to agroecosystems.

## 2. Species richness and ecological representation of predatory Coccinellidae

### 2.1 Global taxonomic richness and distribution

The family Coccinellidae is globally distributed and includes predatory, fungivorous and phytophagous lineages. Broad family-level estimates of approximately 6,000 described species are widely used in contemporary literature [4]. From a biological-control perspective, the important point is not the family total but the subset of predatory taxa that occupy crop habitats and respond to prey populations. Genera such as Coccinella, Cheilomenes, Harmonia, Hippodamia, Propylea and related groups contain prominent aphidophagous species, but their abundance and ecological role vary geographically.

### 2.2 Coccinellid richness in India and other major agroecosystems

Poorani's [5] annotated checklist remains a major baseline for the Indian subregion, documenting 400 species, including six subspecies, in 79 genera while excluding Epilachninae. This value should be interpreted as a taxonomic inventory at a particular time rather than a fixed contemporary total. Continuing revision is illustrated by Poorani et al. [6], who documented nine Indian Plotinini species in four genera, including a newly described species and new generic records. These updates show that taxonomic resolution can itself change apparent richness.

### 2.3 Crop- and habitat-associated assemblages

Ladybird assemblages are structured by prey availability, vegetation, habitat complexity, disturbance and season. Human-modified habitats may favour broadly adaptable or introduced species, whereas specialist or endemic taxa can remain restricted to native vegetation. Peñaherrera-Romero et al. [7] provides a clear example: 19 species were detected on San Cristóbal Island, but abundance and habitat association were strongly uneven. This demonstrates why richness should be reported together with composition, abundance and habitat association whenever the objective is to infer ecological function.

### 2.4 From species richness to dominance and persistence

Richness is therefore best viewed as the starting species pool upon which ecological filters act. A species can be present but contribute little to predation because it is rare, seasonally transient, poorly synchronized with prey or subject to high immature mortality. Conversely, a numerically dominant species may contribute disproportionately to pest suppression. The demographic question is consequently not only 'how many species occur?' but 'what fraction of each species survives successive developmental and seasonal filters to form the active reproductive and predatory population?'

## 3. A stage-specific framework for ladybird mortality

### 3.1 Life-stage differences in vulnerability

Eggs are immobile and exposed to thermal and desiccation stress, cannibalism and predation. Early larvae gain mobility but are small, have limited reserves and may be vulnerable to moulting failure, starvation, cannibalism and intraguild predation. Later larvae are stronger competitors and predators but require greater food intake. Pupae are immobile and cannot escape disturbance or natural enemies. Adults are more mobile and behaviourally flexible, yet face starvation, parasitoids, pathogens, pesticide exposure and overwintering stress. These differences make mortality intrinsically stage-specific.

### 3.2 Recruitment and demographic bottlenecks

Agarwala[8] quantified stage-specific mortality in Anisolemnia dilatata, Coccinella transversalis and C. septempunctata. All three experienced their highest mortality in the first larval instar, but the specialist A. dilatata showed an especially severe early bottleneck: cumulative egg plus first-instar mortality was approximately 50%, total immature mortality exceeded 83%, and only about 10% recruited to adulthood. The two generalists showed 32–36% overall survival to adulthood, with cannibalism contributing importantly to early mortality. These data demonstrate that a numerically small difference in early-stage survival can propagate into a large difference in adult recruitment.

### 3.3 Density dependence versus density independence

Density-dependent and density-independent categories are useful heuristics but should not be treated as rigid labels. Cannibalism, competition and parasitoid encounter rates can increase with host or predator density, whereas acute heat or a

rainfall event can impose mortality regardless of population density. Yet interactions blur the distinction: crowding can increase pathogen transmission, prey scarcity can intensify cannibalism, and weather can alter both prey density and encounter rates. For this reason, the present review emphasizes mechanisms and interactions rather than assigning every mortality source to a single category.

## 4. Abiotic constraints on survival

### 4.1 Temperature-dependent development and survival

Temperature is among the best-supported abiotic drivers of coccinellid performance. A global meta-analysis of 82 publications on Harmonia axyridis found large and consistent temperature effects on development, survival and reproductive characteristics [9]. Development rates increased with temperature across the biologically relevant range, whereas survival followed nonlinear optimum curves. In that synthesis, survival optima or plateaux generally occurred within 20–30°C and survival of most stages approached zero near 35°C. These values apply to H. axyridis datasets and should not be generalized as universal thresholds for the family.

Species-specific studies reinforce the need for caution. Wang et al. [10] evaluated Cheilomenes sexmaculata across temperature and photoperiod treatments and found significant effects on preadult development, eclosion, reproduction, longevity and prey consumption. The direction and optimum of individual traits did not necessarily coincide, demonstrating that 'optimal temperature' depends on the fitness component being considered.

### 4.2 Acute heat and thermal extremes

Mean seasonal temperature can conceal short extreme events that are biologically important. Acute heat can reduce egg hatch, immature survival and subsequent adult performance even when exposure is brief. The relevant demographic consequence is therefore not only immediate mortality but also carry-over effects: individuals surviving heat stress may reach adulthood with altered fecundity, longevity or stress resistance. Future work should distinguish chronic warming from short heat-wave exposure and should report stage-specific exposure histories.

### 4.3 Low temperature, diapause and overwintering

Temperate coccinellids use diapause and aggregation to survive periods when prey is scarce and temperatures are low. These strategies reduce activity and energy expenditure but create a prolonged period during which stored reserves, body condition and pathogen exposure can determine survival. Overwintering is therefore a demographic filter connecting one crop season with the next rather than merely a period of inactivity.

### 4.4 Rainfall and physical disturbance

Rainfall can affect ladybirds directly through mechanical disturbance and indirectly through changes in prey abundance, plant growth and foraging opportunity. Eggs and small larvae on exposed foliage are logically more susceptible to wash-off than mobile adults, but quantitative field estimates of cause-specific rainfall mortality are much less abundant than thermal studies. Accordingly, rainfall should be treated as a plausible and context-dependent mortality driver rather than assigned a universal mortality rate.

### 4.5 Relative humidity and moisture stress

Moisture influences water balance, egg viability, activity and pathogen transmission. However, the evidence does not support a single family-wide 'optimal relative humidity' interval. Effects depend on species, temperature, developmental stage and exposure duration. Humidity is especially important through interaction with pathogens and overwintering aggregations, where close contact can facilitate transmission of ectoparasitic fungi.

### 4.6 Interactions among climatic variables

Temperature, moisture and rainfall rarely operate independently in crop systems. Hot-dry conditions can impose water stress; warm-humid conditions can alter disease risk; rainfall can simultaneously change microclimate, prey density and foraging time. Multifactor experiments remain comparatively scarce, which limits prediction under climate change. Mechanistic models should therefore incorporate both direct physiological effects and indirect prey-mediated effects.

## 5. Resource limitation and predator–prey dynamics

### 5.1 Prey availability and prey quality

Aphidophagous ladybirds depend on suitable prey not only for maintenance but for development and reproduction. Prey scarcity can reduce larval growth, delay development, suppress oviposition and promote dispersal. Prey quality is equally important: different aphid species or alternative foods can alter development and fecundity even when prey is abundant. Consequently, prey density alone is an incomplete measure of habitat suitability.

### 5.2 Functional responses to prey density

Pervez and Omkar [11] experimentally evaluated Cheilomenes sexmaculata, Propylea dissecta and Coccinella transversalis across densities of two aphid prey species. Logistic-regression analysis indicated a decelerating Type II functional response in all three predators. Consumption increased as prey density increased but saturated at high density, consistent with constraints imposed by handling and processing time. The study also demonstrates why universal claims such as 'a ladybird consumes 50–100 aphids per day' are inappropriate: consumption depends on predator species, prey species, stage, temperature and prey density.

### 5.3 Nutritional stress, reproduction and starvation

When prey declines, the consequences extend beyond immediate starvation. Adults may allocate fewer resources to reproduction, delay oviposition or leave the habitat, while larvae may switch to conspecific or heterospecific prey. These responses can reduce local recruitment before starvation mortality becomes obvious. Resource limitation therefore acts both directly and through behavioural pathways.

### 5.4 Dispersal and habitat tracking under prey depletion

Adult mobility allows ladybirds to track ephemeral prey patches, but dispersal can also reduce local biological-control function. A crop may lose predators precisely when prey declines temporarily, creating a lag before recolonization if the pest rebounds. Landscape heterogeneity, refuges and alternative prey can therefore influence persistence by buffering resource discontinuity.

## 6. Cannibalism: mortality under resource competition

### 6.1 Ecological drivers of cannibalism

Cannibalism is widespread among aphidophagous Coccinellidae and should not be treated simply as abnormal laboratory behaviour. Classic work on Adalia bipunctata and subsequent studies show that cannibalism can occur in the field and becomes advantageous under prey scarcity because conspecific eggs or larvae provide concentrated nutrients when aphids are unavailable [12].

### 6.2 Stage-specific susceptibility

Khan and Yoldaş [13] examined Coccinella septempunctata with and without Acyrthosiphon pisum. Eggs and first- and second-instar larvae were cannibalized by adults in both conditions, but the level was inversely related to aphid availability. Older larvae consumed more eggs and younger larvae when aphids were absent. Thus, vulnerability reflects developmental asymmetry: small immobile or weak stages become prey for larger conspecifics.

### 6.3 Effects of prey scarcity and predator density

Prey scarcity increases encounter consequences because conspecific prey becomes relatively more valuable. Density can further increase encounter frequency, but cannibalism should not be described as purely density-driven; food availability, age structure and developmental stage strongly modify its expression. Recent stage-specific mortality data show that cannibalism can contribute materially to early mortality in generalist species [8].

### 6.4 Cannibalism as mortality versus adaptive resource acquisition

At the individual-victim level, cannibalism is unequivocal mortality. At the cannibal level, it can provide nutrition, reduce competition and permit survival during prey shortages. Population-level consequences therefore depend on whether the nutritional and competitive benefits to survivors offset lost recruitment. The most defensible interpretation is that cannibalism is a conditional demographic process with both mortality and survival consequences, not an inherently stabilizing mechanism.

## 7. Intraguild predation and interspecific interference

### 7.1 Mechanisms and stage asymmetry

Intraguild predation (IGP) occurs when predators that share an extraguild prey also consume one another. Size asymmetry and developmental stage strongly affect outcome. Eggs and early larvae are commonly vulnerable, whereas larger larvae and adults are more likely to act as intraguild predators.

### 7.2 Role of extraguild prey availability

Nóia et al. [14] experimentally examined Harmonia axyridis and Coccinella undecimpunctata. Increasing extraguild aphid prey reduced the magnitude and symmetry of IGP, although vulnerable stages remained at risk. Predation on a single intraguild prey individual fell from more than 80% without extraguild prey to 6–53% at higher prey densities, depending on the interaction. This is direct evidence that resource availability modifies mortality generated by predator–predator interactions.

### 7.3 Native–invasive interactions

Semi-field experiments comparing H. axyridis, Adalia bipunctata and C. septempunctata found H. axyridis to be a particularly successful intraguild predator. It won 86% of heterospecific battles against A. bipunctata and 44% against C. septempunctata in observed encounters [15]. Such asymmetry can contribute to competitive advantage, but encounter frequency in real vegetation is lower than in confined arenas.

### 7.4 Laboratory potential versus realized field IGP

Field evidence cautions against assuming that strong laboratory IGP automatically explains community change. In sentinel-egg experiments, native ladybird eggs often experienced greater predation than H. axyridis eggs, yet video surveillance did not identify exotic coccinellids as the predators; harvestmen and slugs accounted for many attacks [16]. Thus, IGP potential is real, but realized field mortality depends on habitat, encounter rate and the broader predator community.

## 8. Predators and parasitoids as external mortality agents

### 8.1 Predation across developmental stages

Coccinellids possess chemical defences and aposematic coloration, but these do not eliminate predation. Eggs and small larvae are especially exposed to generalist arthropod predators. Field sentinel studies show that substantial egg predation can occur and that the responsible predators may include taxa not normally emphasized in ladybird-centred food webs. Predation should therefore be quantified empirically rather than inferred only from predator presence.

### 8.2 Parasitoid diversity and host range

Parasitoids can reduce survival and reproduction without producing a uniform field parasitism rate. The braconid Dinocampus coccinellae is the best-studied example and attacks multiple coccinellid hosts. Local parasitism can nevertheless be low. In northern Italy, field-collected H. axyridis, C. septempunctata, A. bipunctata and Hippodamia variegata showed D. coccinellae parasitism rates of 2.3–6.2%, demonstrating why generalized values such as 5–20% should not be used as family-wide expectations [17].

### 8.3 Dinocampus coccinellae as a model parasitoid

D. coccinellae is particularly informative because host exploitation continues beyond simple mortality. The parasitoid develops within the beetle, emerges and forms a cocoon beneath the host. In some host associations the ladybird

remains alive and displays tremors while positioned over the cocoon, a phenomenon often termed bodyguard behaviour.

### 8.4 Parasitoid-mediated fitness and behavioural effects

Dheilly et al. [18] demonstrated that D. coccinellae paralysis virus (DcPV), associated with the parasitoid, replicates in host nervous tissue and correlates with neuropathy and paralytic symptoms in Coleomegilla maculata. Viral clearance correlated with recovery of normal behaviour. This work illustrates that parasitoid effects can be mediated by associated microorganisms and can alter behaviour as well as survival.

## 9. Pathogens and disease-mediated mortality

### 9.1 Fungal and other microbial associates

Ladybirds interact with diverse microorganisms ranging from beneficial symbionts to parasites and pathogens. The demographic outcome depends on host species, microbial identity, transmission route, season and physiological condition. Recent reviews emphasize that microbial associations are an underappreciated component of ladybird persistence in agricultural habitats [4].

### 9.2 Hesperomyces–ladybird interactions

The Laboulbeniales ectoparasite historically referred to as Hesperomyces virescens has been studied extensively on H. axyridis. Transmission can occur through close physical contact, including mating and aggregation. The most compelling evidence for demographic impact comes from overwintering experiments rather than simple prevalence records.

### 9.3 Aggregation, transmission and overwintering

Knapp et al. [19] experimentally investigated overwintering H. axyridis and found winter survival of 60% in heavily infected individuals compared with 79.8% in uninfected individuals. Infection was the only variable in their combined survival analysis that significantly affected winter survival. Because overwintering aggregations increase contact opportunities, seasonal aggregation can simultaneously function as a survival strategy and a transmission environment.

### 9.4 From infection to host mortality: physiological mechanisms

The same study found that body-mass loss tended to be higher in infected beetles, whereas measured haemolymph immune parameters were only weakly affected by infection. The authors therefore considered energy exhaustion unrelated to a major immune-system challenge the most probable explanation for increased winter mortality [19]. The mechanism should be described as evidence-supported inference rather than as proof that the fungus directly 'drains' host energy reserves.

## 10. Anthropogenic survival constraints in agroecosystems

### 10.1 Insecticide-induced mortality

Agricultural chemicals add a mortality filter that differs from natural environmental variation because exposure is management-dependent. Toxicity can vary by orders of magnitude among active ingredients. For C. septempunctata larvae, a comparative study of diamide insecticides found broflanilide substantially more toxic than chlorantraniliprole or tetrachlorantraniliprole, with reported pre-imaginal LR50 values of 0.0943, 42.078 and 289.516 g active ingredient ha−1, respectively [20]. Such results emphasize that pesticide compatibility must be assessed at the compound and life-stage level.

### 10.2 Sublethal effects on development, reproduction and predation

Survivors of pesticide exposure may experience delayed development, reduced feeding, altered movement or lower reproduction. These effects can decrease biological-control function without causing conspicuous mortality. Risk assessment based only on acute adult mortality can therefore underestimate demographic impact.

### 10.3 Habitat simplification and resource discontinuity

Simplified landscapes can reduce alternative prey, refuge sites and continuity of resources. Conversely, heterogeneous habitats and semi-natural vegetation may provide overwintering sites, floral resources or alternative prey. Habitat management therefore influences survival indirectly by modifying the probability that predators encounter suitable resources through time.

### 10.4 Conservation-compatible crop management

Conservation biological control should combine selective pesticide use, protection of refuge habitats and temporal matching of management operations with predator activity. The objective is not merely to maximize ladybird abundance but to preserve recruitment and persistence of locally effective species while avoiding practices that amplify mortality at vulnerable stages.

## 11. Integrating mortality across the life cycle

### 11.1 Interactions among abiotic and biotic mortality factors

Mortality sources form a network rather than a list. Temperature changes developmental rate and therefore exposure time; prey scarcity changes dispersal, reproduction, cannibalism and IGP; aggregation protects against some abiotic stresses while facilitating pathogen transmission; and pesticides can interact with nutritional or thermal stress. The effect of one factor can therefore depend on the state created by another.

### 11.2 Carry-over effects between developmental stages

A major limitation of many experiments is that they end when immediate survival is scored. Heat, starvation, pesticide exposure or parasitism during immature development can alter adult body condition, fecundity and longevity. These carry-over effects mean that stage-specific mortality should include both death within a stage and reduced probability of successful reproduction after surviving that stage.

### 11.3 Compensatory versus additive mortality

Mortality factors can be compensatory when the removal of individuals reduces later competition or cannibalism, or additive when independent hazards remove individuals that would otherwise survive. Distinguishing these processes is essential for predicting population consequences. Summing percentages from separate experiments is therefore inappropriate; integrated life tables and field manipulations are needed.

### 11.4 From individual mortality to population persistence

Population persistence emerges from the product of survival probabilities across successive stages, modified by reproduction, dispersal and seasonal carry-over. A severe bottleneck at one stage can dominate adult recruitment even when later stages have high survival. This is why the first-instar bottleneck documented by Agarwala [8] is demographically important and why richness data alone cannot predict predator persistence.

### 11.5 Consequences for realized pest suppression

Biological-control function requires both sufficient predator density and appropriate timing relative to pest populations. Functional response describes per-capita feeding under given prey densities, whereas demographic persistence determines how many predators are available to express that response. Effective pest suppression therefore reflects the intersection of feeding performance, recruitment, retention and survival.

## 12. Implications for biological control

Biological-control programmes should select species or populations whose thermal and prey requirements match the target agroecosystem rather than assuming that broadly effective laboratory predators will persist under field conditions.

Augmentative releases should account for stage-specific vulnerability. Releasing large numbers cannot compensate efficiently for predictable early-stage mortality if prey, microclimate or pesticide exposure remain unsuitable.

Conservation programmes should maintain resource continuity and refuges, especially across periods of low pest density, while minimizing broad-spectrum pesticide exposure during predator establishment.

Mass-rearing systems should monitor cannibalism, parasitoids and pathogens because high-density rearing can amplify encounter-mediated mortality and disease transmission.

Evaluation of biological-control agents should combine functional-response measurements with demographic endpoints such as immature survival, adult recruitment, fecundity and overwinter persistence.

## 13. Knowledge gaps and research priorities

Cause-specific field life tables are scarce. Laboratory studies identify mechanisms, but their relative contribution to mortality under realistic crop conditions remains poorly quantified.

Indian and broader South Asian agroecosystems require updated, crop-specific demographic studies that connect coccinellid species identity with stage-specific survival and seasonal persistence.

Rainfall and humidity effects are less quantitatively resolved than temperature effects. Experiments should separate direct physical mortality from prey-mediated and pathogen-mediated pathways.

Multifactor experiments are needed. Temperature, food limitation, pesticides and natural enemies are usually studied independently even though they co-occur in the field.

Carry-over effects require greater attention. Survival to the next stage is insufficient if early stress substantially reduces adult reproduction or predatory performance.

IGP research should bridge laboratory potential and realized field interaction through direct observation, molecular gut-content methods and spatially realistic experiments.

Parasitoid and pathogen studies should quantify demographic consequences across seasons and host species rather than relying on prevalence alone.

Climate-change research should move beyond mean warming to include heat waves, altered rainfall regimes and mismatches between prey and predator phenology.

Future syntheses would benefit from standardized reporting of stage, temperature, prey density, exposure duration and survival denominators, enabling formal meta-analysis.

**Table 1:** Representative evidence linking species richness, assemblage structure and ecological representation in Coccinellidae

| Study/region | System | Key evidence | Interpretive value |
|---|---|---|---|
| Poorani[5], Indian subregion | Taxonomic checklist | 400 species (including six subspecies), 79 genera; Epilachninae excluded | Baseline Indian taxonomic inventory; not a fixed current total |
| Peñaherrera-Romero et al.[7], Galápagos | Natural and human-modified habitats | 19 species; endemic taxa scarce/restricted; C. sanguinea prevalent; C. sexmaculata associated with disturbed habitats | Richness does not imply equal abundance or persistence |
| Poorani et al.[6], India | Plotinini revision | Indian Plotinini revised from 6 species/3 genera to 9 species/4 genera; new species described | Taxonomic revision changes apparent richness |

**Table 2:** Representative evidence for abiotic survival constraints

| Species | Stage/factor | Conditions/evidence | Response | Reference |
|---|---|---|---|---|
| Harmonia axyridis | Multiple stages; temperature | Global meta-analysis of 82 publications; 14–35°C inclusion range | Temperature strongly affected development, survival and reproduction; survival optima/plateaux generally 20–30°C; most stages approached zero survival near 35°C | Raak-van den Berg et al.[9] |
| Cheilomenes sexmaculata | Preadult/adult; temperature & photoperiod | Five temperature and five photoperiod regimens | Development, eclosion, reproduction, longevity and predation responded to temperature/photoperiod; trait-specific responses differed | Wang et al.[10] |
| Harmonia axyridis | Overwintering; infection × season | Infected vs uninfected adults | Heavily infected winter survival 60% vs 79.8% in uninfected beetles | Knapp et al.[19] |

**Table 3:** Representative evidence for biotic mortality and survival constraints

| Species/system | Factor | Quantitative or mechanistic evidence | Demographic implication | Reference |
|---|---|---|---|---|
| C. sexmaculata, P. dissecta, C. transversalis | Prey density / functional response | All three showed Type II functional responses across tested prey densities | Per-capita feeding saturates; prey density affects performance but feeding is not proportional indefinitely | Pervez & Omkar[11] |
| C. septempunctata | Cannibalism | Eggs and L1–L2 cannibalized by adults; cannibalism inversely related to aphid availability | Prey scarcity shifts mortality toward vulnerable conspecific stages | Khan & Yoldaş[13] |
| H. axyridis vs C. undecimpunctata | IGP | Predation >80% without extraguild prey, declining to 6–53% at higher prey densities depending on interaction | Extraguild prey modifies IGP magnitude | Nóia et al.[14] |
| H. axyridis, A. bipunctata, C. septempunctata | IGP | H. axyridis won 86% and 44% of heterospecific battles against A. bipunctata and C. septempunctata | Strong asymmetric IGP potential in semi-field encounters | Katsanis et al.[15] |
| Four coccinellid spp., northern Italy | Parasitoid | D. coccinellae field parasitism 2.3–6.2% | Local parasitoid pressure can be modest and variable | Dindo et al.[17] |
| H. axyridis | Fungal ectoparasite | Winter survival 60% heavily infected vs 79.8% uninfected | Infection reduces seasonal carry-over into next population | Knapp et al.[19] |

**Table 4:** Stage-specific mortality and demographic interpretation

| Species | Egg/early stage | Later immature stages | Adult recruitment / endpoint | Principal inference | Reference |
|---|---|---|---|---|---|
| Anisolemnia dilatata | Egg + L1 cumulative mortality ~50%; L1 highest mortality | Further immature losses; total mortality >83% | ~10% recruitment to adulthood | Severe early developmental bottleneck in specialist | Agarwala[8] |
| Coccinella transversalis | L1 highest mortality | Mortality more evenly distributed than specialist; cannibalism important early | Overall survival to adulthood within 32–36% range reported for generalists | Behavioural flexibility buffers but does not eliminate early losses | Agarwala[8] |
| Coccinella septempunctata | L1 highest mortality; eggs/young larvae susceptible to cannibalism | Cannibalism and other losses distributed across development | Overall survival to adulthood within 32–36% range reported for generalists | Prey-mediated cannibalism contributes to recruitment loss | Agarwala[8]; Khan & Yoldaş8,13 |

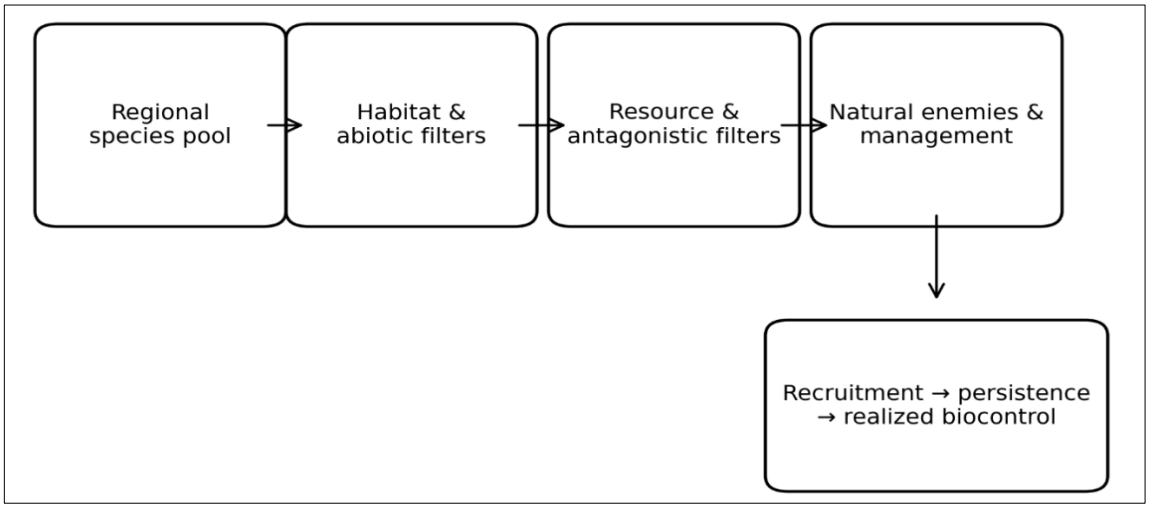



**Fig 1:** Conceptual transition from regional species richness to realized biological-control function. The regional species pool is filtered by habitat, abiotic conditions, resource availability, antagonistic interactions, natural enemies and agricultural management. Stage-specific survival determines recruitment, population persistence and the predator population available for pest suppression

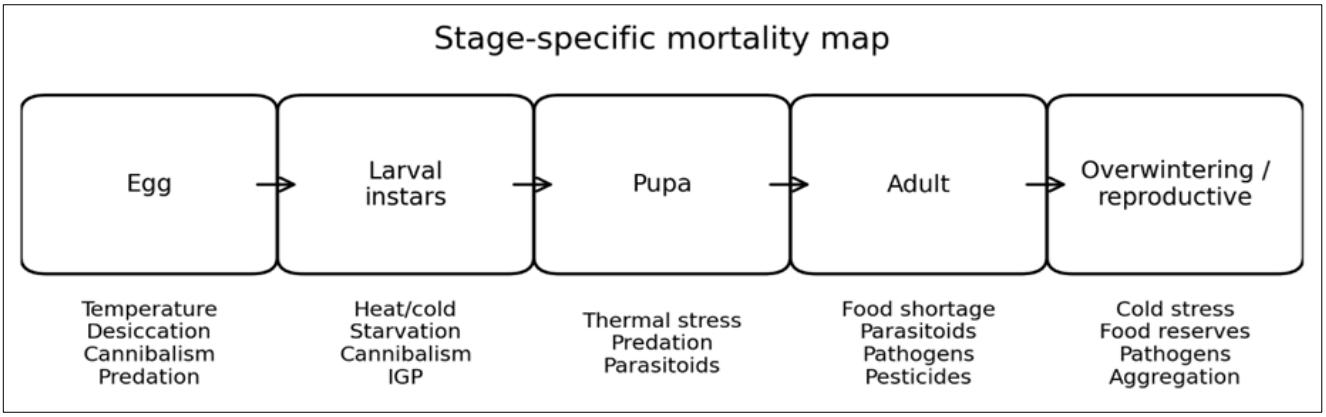



**Fig 2:** Stage-specific mortality map for predatory ladybird beetles. Mortality factors are mapped onto egg, larval instars, pupa, adult and overwintering/reproductive stages. The framework emphasizes that susceptibility is conditional and species-specific rather than assigning universal mortality rankings

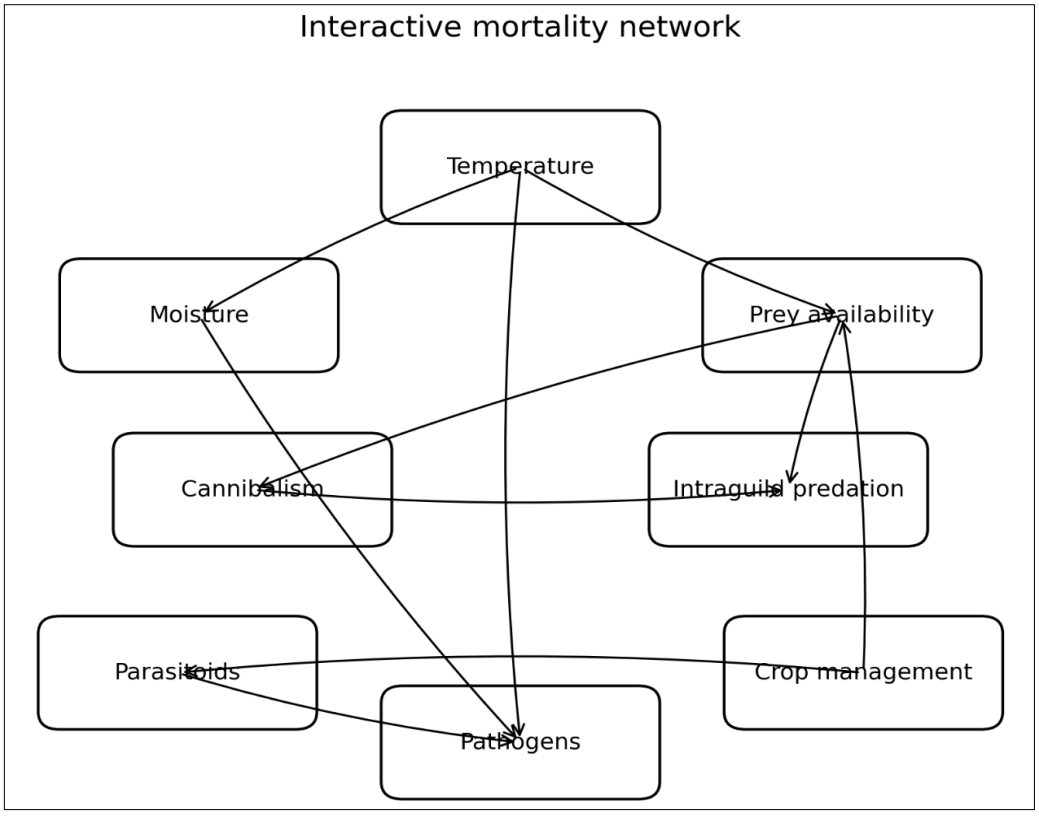



**Fig 3:** Interactive mortality network. Temperature, moisture, prey availability, cannibalism, intraguild predation, parasitoids, pathogens and crop management are connected through direct and indirect pathways. Arrows denote mechanistic influence, not necessarily positive statistical correlation

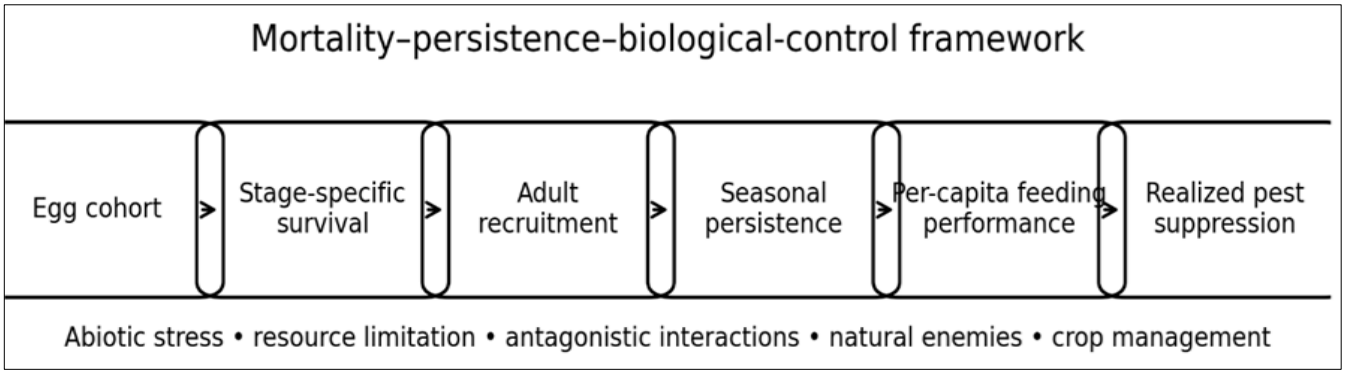



**Fig 4:** Mortality–persistence–biological-control framework. Sequential survival from egg cohort through adult recruitment and seasonal persistence determines the number of predators available to express per-capita feeding performance and thereby realized pest suppression

## 14. Conclusions

Predatory Coccinellidae combine high taxonomic richness with strong ecological heterogeneity. The presence of many species in a region or crop does not guarantee that those species will persist or contribute equally to pest suppression.

Survival is filtered sequentially across the life cycle. Temperature, moisture and extreme weather impose physiological and physical constraints; prey availability governs growth, reproduction and movement; cannibalism and intraguild predation redistribute mortality within predator assemblages; external predators, parasitoids and pathogens remove additional individuals; and agricultural management can intensify or alleviate these pressures.

Stage-specific evidence is particularly important because early mortality can create demographic bottlenecks that determine adult recruitment. Recent life-table results showing first-instar mortality as the largest loss in several aphidophagous species provide a useful model for future field studies.

The most informative conceptual pathway is therefore species richness → stage-specific survival → recruitment → population persistence → realized biological-control function. Integrating these steps provides a stronger basis for conservation and deployment of predatory ladybirds than richness counts or feeding-rate measurements considered alone.

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